STUDIES IN NEOTROPICAL PALEOBOTANY. VII. THE LOWER MIOCENE COMMUNITIES OF PANAMA—THE LA BOCA FORMATION[1]

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ABSTRACT

Thirty-nine palynomorphs have been identified from among 54 forms recovered from the lower Miocene La Boca Formation in the Canal region of Panama. These are ascomycete cleistothecia, the dinoflagellates *Spiniferites* and *Operculodinium*, *Lycopodium*, *Selaginella*, *Cyathea*, *Pteris* (types 1 and 2), cf. *Antrophyum*, other trilete fern spores (types 1–3), monolete fern spores (types 1–5), Gramineae, Palmae (*Attalea*, *Manicaria*, and *Synechanthus* types), *Ilex*, cf. *Aguiaria*, cf. *Ceiba*, *Pseudobombax*, *Alchornea*, *Alfaroa/Engelhardia*, *Crudia*, *Utricularia*, Malpighiaceae (types 1–5), Malvaceae, *Rhizophora* (constituting 67–88% of five samples counted), Rubiaceae (types 1 and 2), and *Pelliciera*. The flora is estuarine in aspect, and consistent with three other lower Miocene assemblages (Uscari, Culebra, Cucaracha), reflects low-lying volcanic islands fringed seaward by mangroves, with freshwater fern and palm swamp marshes in the lowlands and versions of the tropical wet, tropical moist, and premontane forests on the adjacent slopes. There is no palynological evidence for communities of drier to arid aspect (including savannahs) or of high altitudes; elevations of 1,200 to 1,500 m would accommodate all taxa present in the La Boca and other fossil floras. The affinity of the flora is distinctly with Central America and areas to the north. With the exception of *Crudia*, all genera occur in the modern vegetation of Panama, and consequently the paleoclimate, in agreement with Tertiary paleotemperature curves, was similar to that prevailing today in coastal, lowland, and moderate-altitude tropical habitats in southern Central America.

The La Boca Formation is the third in a series of three stratigraphically and lithologically similar formations from the geologically complex Canal region of Panama yielding well-preserved fossil pollen and spores. The Culebra Formation is oldest (basal) and is overlain by the Cucaracha Formation. The La Boca does not anywhere lie directly on the Cucaracha, but it interfingers (viz., is contemporaneous) with the Pedro Miguel Formation, which overlies the Cucaracha elsewhere in the Canal region. Age estimates are based primarily on molluscan (Woodring, 1957–1982) and ostracod (Van den Bold, 1972, 1973) data which suggest an early Miocene age for the three formations.

The La Boca outcrops along both sides of the Panama Canal from the Pacific entrance to the Las Cascadas Reach. The sediments were deposited in an estuarine environment and include an alternating sequence of mudstones, siltstones, sandstones, lignitic shales, tuffs (waterlain volcanic ash), and limestones typical of that environmental setting. The presence of the coralliferous Emperador limestone member in the lower part of the formation and *Rhizophora*-containing lignitic shales indicate deposition in warm temperate to tropical, shallow seas and in adjacent coastal, brackish-water habitats.

Fifty-four samples were collected from two exposures of the La Boca Formation along the Las Cascadas Reach in September 1967 (latitude 9°04′N, longitude 79°40′W; ground elevation 52.7 m). Locality A (samples 1–26) was at Canal marker 1600 (1766 in the new marking system), and locality B (samples 27–54) at markers 1622 (1788), 1625 (1791), and 1627 (1793). Since that time the Canal has been widened from 90 m to 155 m, and compared with the present physiography, the 1967 samples were collected about 25 m up and 60 m out over the present Canal. The beds dipped back into the slope at a 20–25° angle so that now

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the same lignite layers are nearly at water level. Other details of the collecting site and geology of the area are summarized in Graham et al. (1985: 495–502).

Materials and Methods

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to locality, sample number, and slide number (e.g., Pan A 5-1). Of the 54 samples collected, 20 contained fair to well-preserved palynomorphs (locality A—5, 14, 16, 17, 19, 20, 21; locality B—27, 28, 29, 30, 33, 34, 35, 45, 46, 47, 50, 52, 54). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF C-29). The tabulations in Table 1 are based on five representative samples (14, 16, 20, 21, 50) containing diverse and well-preserved palynomorphs. All materials are deposited in the palynology collections at Kent State University.

Systematics

Thirty-nine palynomorphs have been identified from the La Boca Formation (Table 1) in addition to 15 others that cannot presently be identified (unknowns 1–15). Most of the specimens have been recovered from other Tertiary formations in the Gulf/Caribbean region and discussed in previous publications, hence the material presented here is synoptic. These formations and references are as follows: Gatuncillo (middle(?) to late Eocene, Panama; Graham, 1985); San Sebastian (middle to late Oligocene, Puerto Rico; Graham & Jarzen, 1969); Uscari (early Miocene, Costa Rica; Graham, 1987a, b); Culebra (early Miocene, Panama; Graham, 1988a), and Cucaracha (early Miocene, Panama; Graham, 1988b). Present ranges of the modern analogs within the Neotropics and ecological data are based on field observations, personal communication with specialists, and the literature, especially Croat (1978), D'Arcy (1987), Hartshorn (1983), Tryon & Tryon (1982), and Woodson & Schery (1943–1980). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), used by Croat (1978) and Hartshorn (1983) for describing the plant communities of Panama and Costa Rica. In instances where the modern analogs extend into South America, their altitudinal ranges and community affiliations may differ slightly from their Central American occurrences. The data for Central America are considered first in paleocommunity and paleoenvironmental reconstruction of the La Boca flora, since communities in South America are more distant and were isolated from Central America until about 3 Ma.

FUNGI

Ascomycete cleistothecium (Fig. 1). Flattened, circular, multicellular, cells cubical, 6 × 9 μm, outer and some lateral walls of peripheral (marginal) cells thickened, center opaque (solid?), cells disrupted along outer edge, forming slitlike opening 35 μm long (attachment scar?); 124 μm.

Reproductive structures of the Plectomycetes group of ascomycete fungi are frequent in Gulf/Caribbean Tertiary deposits but never in large numbers. Although entire specimens are relatively rare, fragments are present in almost all samples. Another type with radially aligned cells and marginal spines was recovered from the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a, fig. 1).

PYRROPHYTA

Spiniferites (Figs. 2, 3). These dinoflagellate cysts, as fossils referable to *Spiniferites*, are common in the Tertiary and extend back to the Early Cretaceous. They are produced by some species of the extant *Gonyaulax* group (Evitt, pers. comm., 1987).

Operculodinium centrocarpus (Fig. 4). This is also a common Tertiary form produced by the modern *Gonyaulax grindleyi* (= *Protoceratium reticulatum*) and a frequent associate of *Spiniferites* in the Miocene. According to Evitt (pers. comm., 1987), "These two cyst types are common constituents of Tertiary nearshore sediments. They occur, virtually to the exclusion of other forms, in the Miocene Monterrey Formation in California (*Spiniferites* much the more abundant), and together with a very rich associated assemblage in the Calvert Formation along the east coast. It would be entirely plausible to find them in estuarine deposits of Miocene age virtually anywhere. No examples of *Spiniferites*, which has a very distinctive and easily recognized morphology (at least at the generic level), have been found in fully freshwater sediments."

LYCOPODIACEAE

Lycopodium (Fig. 5). Amb triangular, apices rounded; trilete, laesurae straight, narrow, ca. 20–22 μm long, extending to spore margin, inner margin entire, distal surface with numerous circular punctae ca. 1 μm diam., proximal face laevigate; wall 1–1.5 μm thick; 40 μm.

These spores are similar to those of *L. reflexum*

TABLE 1. Identification and numerical representation of fossil palynomorphs from the lower Miocene La Boca Formation. Figures are percentages based on counts of 200 specimens from four samples at locality A (14, 16, 20, 21) and one sample at locality B (50). Minus sign (−) indicates specimens are present in the sample but were not encountered in counts of 200. The counts do not include clusters of 20 or more grains of *Rhizophora* found in sample 14, or *Pelliciera* in sample 16.

	Locality A				Locality B
	14	16	20	21	50
Fungi					
Ascomycete cleistothecium					−
Pyrrophyta					
Spiniferites	0.5				1
Operculodinium centrocarpus	1	0.5			
Lycopodiaceae					
Lycopodium	−	−		0.5	
Selaginellaceae					
Selaginella		1	−	−	−
Cyatheaceae					
Cyathea	−	3	1	2.5	
Pteridaceae					
Pteris type 1	−	1		−	−
Pteris type 2	1	1.5	1.5	1	2
Vittariaceae					
Cf. *Antrophyum*	−	1	1	1	2
Trilete fern spores					
Type 1	−	1	0.5		−
Type 2					−
Type 3				−	
Monolete fern spores					
Type 1		0.5	1.5	1	
Type 2	−	1		1.5	−
Type 3		1.5	−	1.5	2.5
Type 4	1	1.5	1.5	−	−
Type 5	1	1.5	1.5		−
Gramineae	−	−			
Palmae					
Attalea type	−	0.5	0.5	1.5	
Maricaria type	1.5	−	1	−	1
Synechanthus type	−	1	1		−
Aquifoliaceae					
Ilex	−	−		−	
Bombacaceae					
Cf. *Aguiaria*		−			
Cf. *Ceiba*		−			
Pseudobombax			−		
Euphorbiaceae					
Alchornea		0.5	−	−	−
Juglandaceae					
Alfaroa/Engelhardia	1	0.5	1	−	2.5

TABLE 1. Continued.

	Locality A				Locality B
	14	16	20	21	50
Leguminosae—Caesalpinioideae					
Crudia	–	2	1	1	1
Lentibulariaceae					
Utricularia	–				
Malpighiaceae					
Type 1		0.5		–	
Type 2	–				1
Type 3				–	–
Type 4	–	–			
Type 5		0.5			
Malvaceae				–	
Rhizophoraceae					
Rhizophora	88	67	76	77.5	74
Rubiaceae					
Type 1	–	1	0.5	–	1
Type 2		1	0.5	–	–
Theaceae					
Pelliciera	2	3	2.5	1	2
Unknowns					
Type 1			–		
Type 2					–
Type 3	–	1	0.5		
Type 4	–				
Type 5	0.5	0.5	0.5		–
Type 6	0.5		–		1
Type 7		–			
Type 8					–
Type 9		–			
Type 10	–	0.5		0.5	
Type 11					–
Type 12				–	
Type 13		0.5	0.5		1
Type 14	–	0.5	–	0.5	
Type 15	0.5	–	1	1	1.5
Other unknowns	1.5	4.5	5	8	6.5

Lam. and *L. linifolium* L. presently occurring in moist shaded habitats in Panama. They have been recovered from the Culebra, Uscari, and Paraje Solo formations, although the Uscari specimens have thicker walls (3–4 μm vs. 1–1.5 μm).

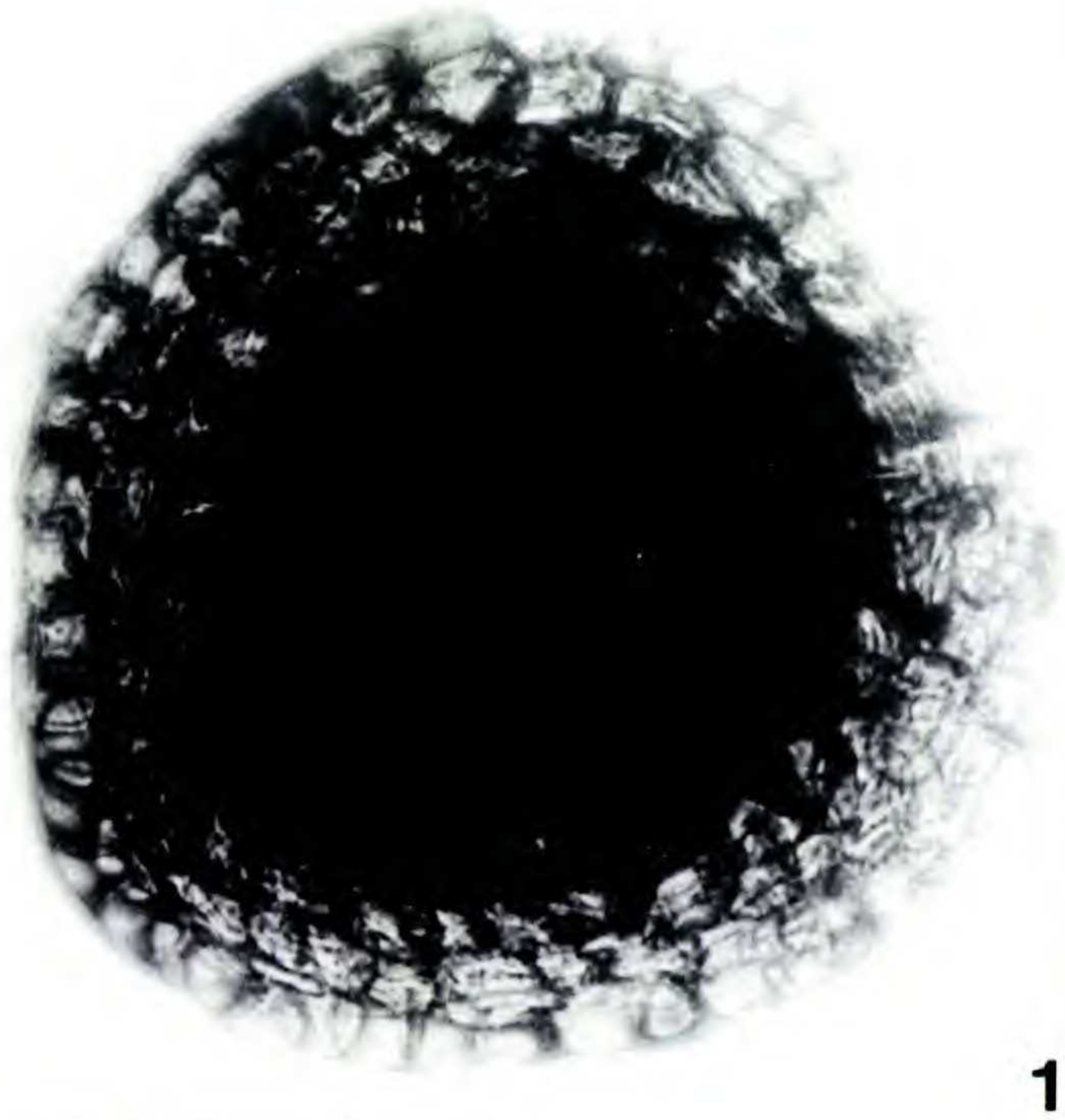
SELAGINELLACEAE

Selaginella (Fig. 6). Spherical, amb circular to oval-triangular; trilete, laesurae frequently obscured by dense sculpture, arms variously developed and spores often appearing monolete, straight, narrow, ca. 20–24 μm long, extending nearly to spore margin; echinate, echinae short (ca. 2–3 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 30–32 μm.

Selaginella is widespread in moist, shaded habitats in the Neotropics. The spores occur in low numbers in the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

CYATHEACEAE

Cyathea (Figs. 10, 13). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 19–21 μm long, extending to or nearly to spore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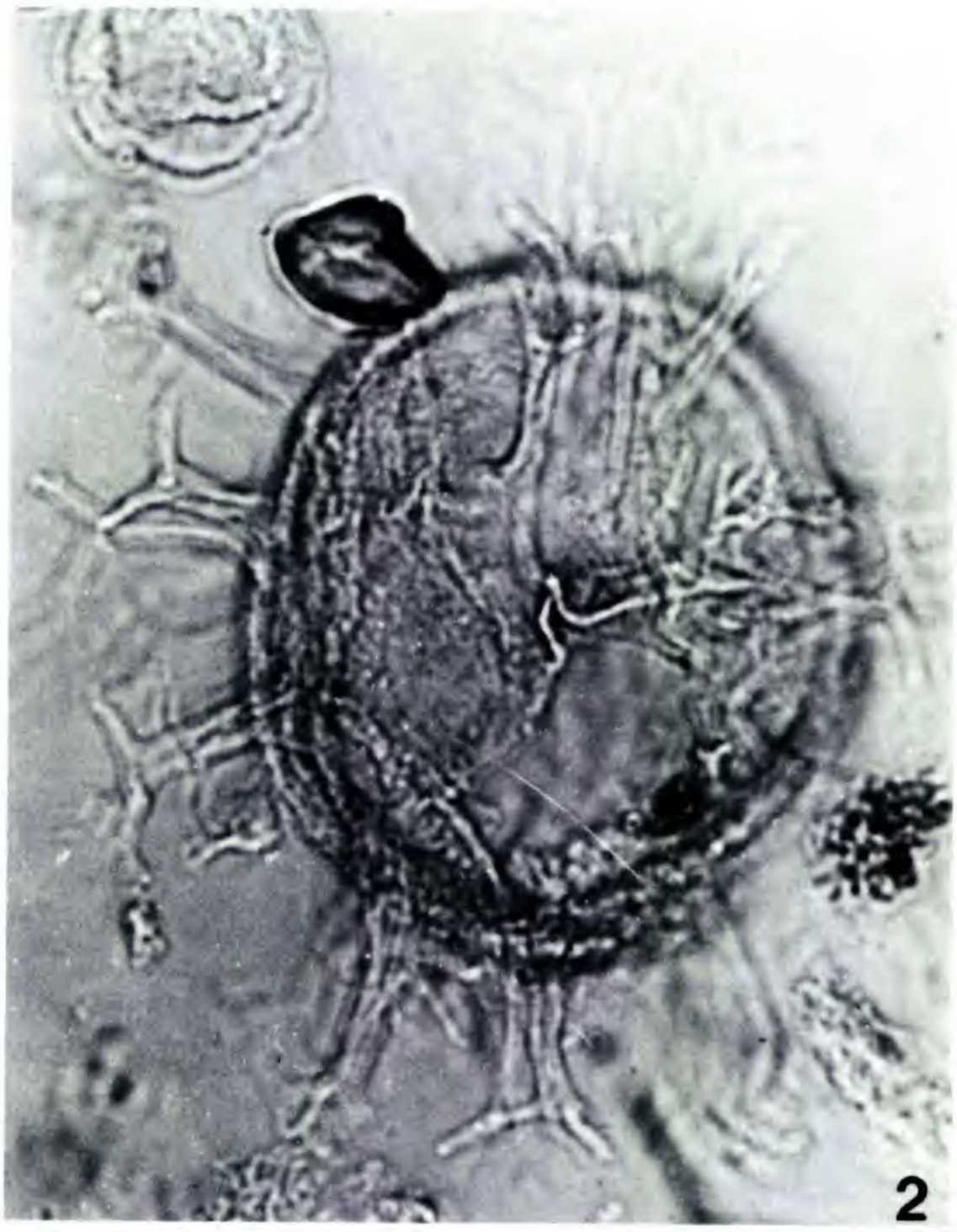
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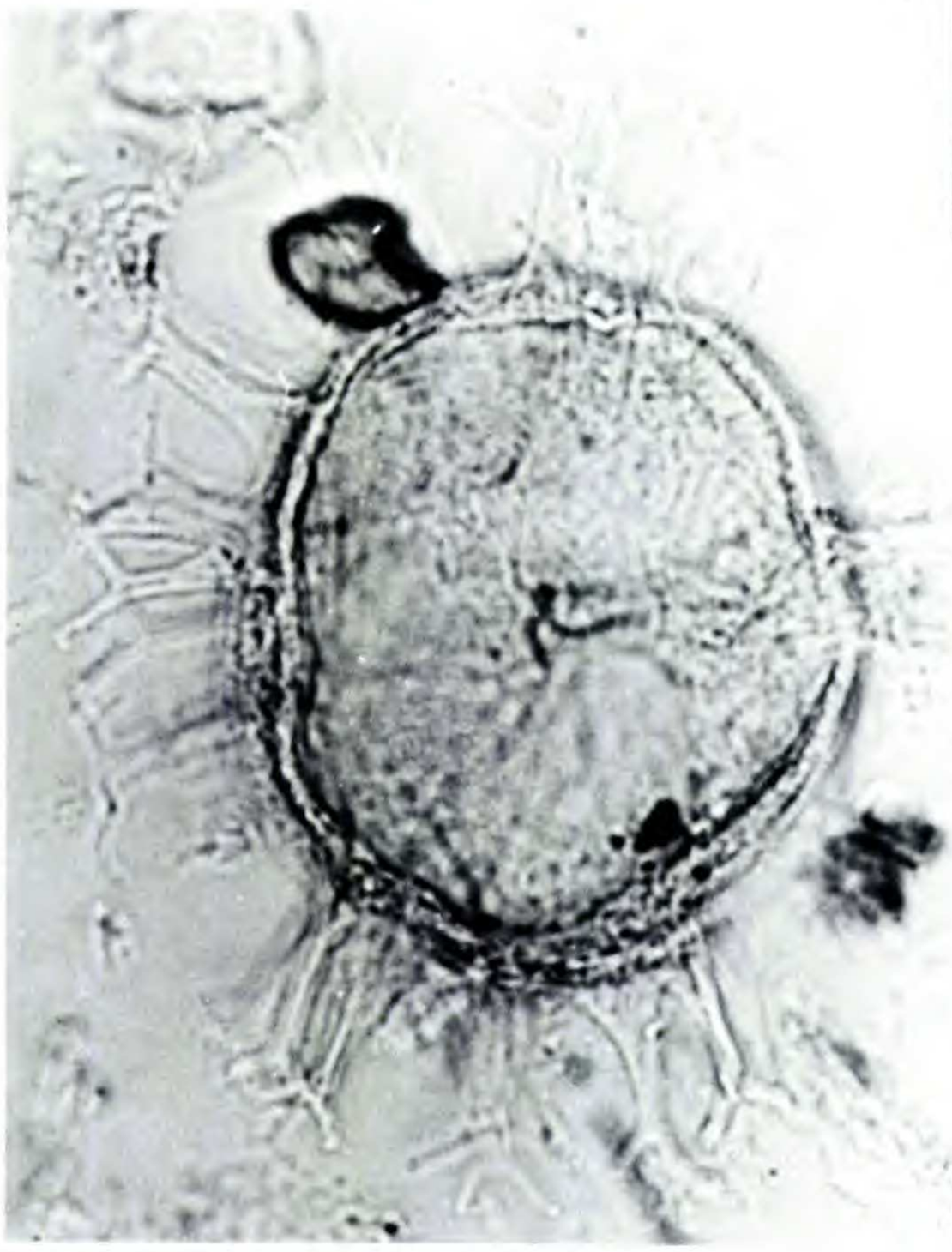
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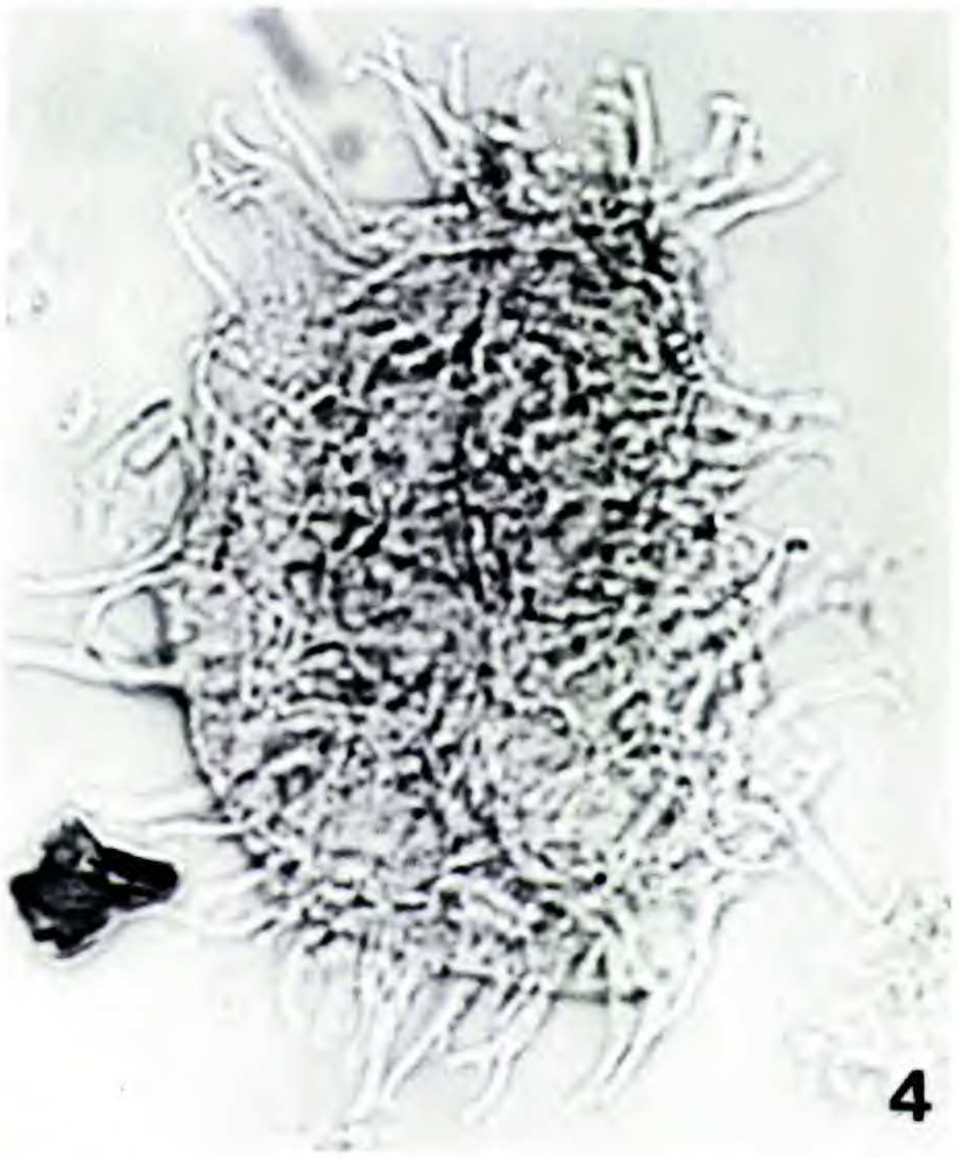
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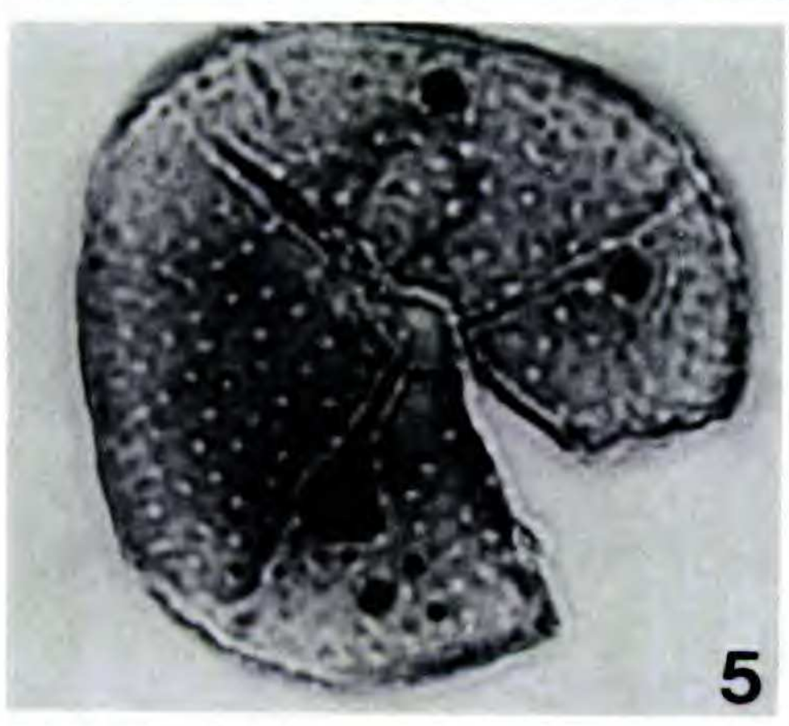
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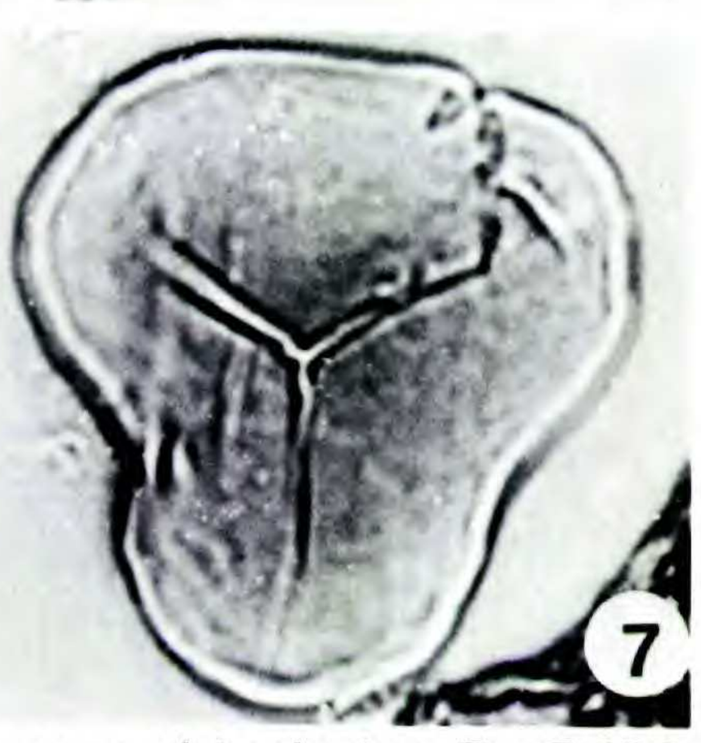
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FIGURES 1–7. Fossil spores from the La Boca Formation, Panama.—1. Ascomycete cleistothecium, Pan B 27-1, ESF C-29, 3–4.—2, 3. *Spiniferites* sp., Pan A 14-1a, ESF R-46, 1–3.—4. *Operculodinium centrocarpus*, Pan A

margin, inner margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 32–36 μm.

Tryon & Tryon (1982: 204) noted that the classification of tree ferns differs among various authors and that the name *Cyathea* has been used to include nearly all members of the family. The labels on reference slides used for identification often reflect this confusion, especially between *Cyathea* and *Alsophila*. A further complication is that the lip surrounding the laesurae is difficult to observe on some fossil specimens because of preservation and/or orientation. According to recent illustrations by Gastony & Tryon (1976) and Tryon & Tryon (1982), trilete, micropunctate forms with a lip often bordered by punctae are referred to *Cyathea*, while forms with a laevigate surface beneath the perine belong to *Alsophila*. Laevigate spores of similar size and morphology lacking the lip and bordering punctae are produced by several extant genera (e.g., species of *Adiantum*). Following this classification, *Cyathea* spores are known from the Culebra, Cucaracha, La Boca, and Paraje Solo formations (as *Alsophila* in the latter; Graham, 1976, figs. 16–18). *Alsophila* is known from the Gatuncillo Formation (Graham, 1985, fig. 10, as trilete fern spore type 1) and from the Paraje Solo Formation (Graham, 1976, fig. 19, as *Cyathea*).

In Central America *Cyathea* grows primarily in low rain forests, montane forests, and cloud forests, usually between 1,500 and 2,000 m.

PTERIDACEAE

Pteris. *Pteris* is a genus of about 250 species, with some 55 occurring in the Neotropics from northern Mexico (Nuevo León) and Florida to Argentina and Chile (Tryon & Tryon, 1982: 334). It usually grows at altitudes below 2,000 m in wet, cloud, or gallery forests. Spores are frequent but not abundant in the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

Type 1 (Figs. 8, 9). Amb oval-triangular, apices rounded, margin entire to slightly undulating; trilete, laesurae straight, narrow, inner margin entire, 23–25 μm long, extending to spore margin; wall with coarse irregular verrucae on distal surface, proximal surface more laevigate, hyaline marginal flange 12–15 μm wide; 62–68 μm.

Type 2 (Figs. 11, 12). Smaller (40–42 μm), the marginal flange narrower (4–5 μm wide), and the verrucae smaller and more numerous.

VITTARIACEAE

Cf. Antrophyum (Fig. 14). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diam., straight, narrow, 12–16 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 50–52 μm.

Antrophyum is represented by about 10 species in the Neotropics, growing in cloud and rain forests usually at elevations between 100 and 1,500 m from Mexico (Hidalgo) through Central America and the Antilles to northern Argentina and southeastern Brazil (Tryon & Tryon, 1982: 360). The spores are similar to those of *Acrostichum aureum* L. (cf. Tryon & Tryon, 1982, figs. 49.10, 12 and 51.8), a species expected in the La Boca and other estuarine formations because it grows in brackish mangrove swamps. The spores of *A. aureum* in our reference material (nine collections) have a granular, scabrate sculpture, while those of *Antrophyum* are more laevigate. The distinction is difficult among fossil specimens, and it is possible that both genera are represented in Gulf/Caribbean Tertiary deposits. Since the fossils are laevigate, however, they are referred to cf. *Antrophyum*. Similar spores are known from the Gatuncillo, San Sebastian (not figured in Graham & Jarzen, 1969), Culebra, Cucaracha, and Paraje Solo (as an unknown in Graham, 1976, fig. 227) formations.

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered for which biological affinities could not be determined. Three of the more distinctive ones are described below.

Type 1 (Fig. 7). Amb oval-triangular, apices rounded, margin entire; trilete, laesurae straight, narrow, inner margin entire, 12 μm long, extending ca. ¾ distance to spore margin; laevigate; wall 1.5 μm thick; 29–32 μm.

These spores are similar to those of several ferns, including *Adiantum*, and cannot be referred to any

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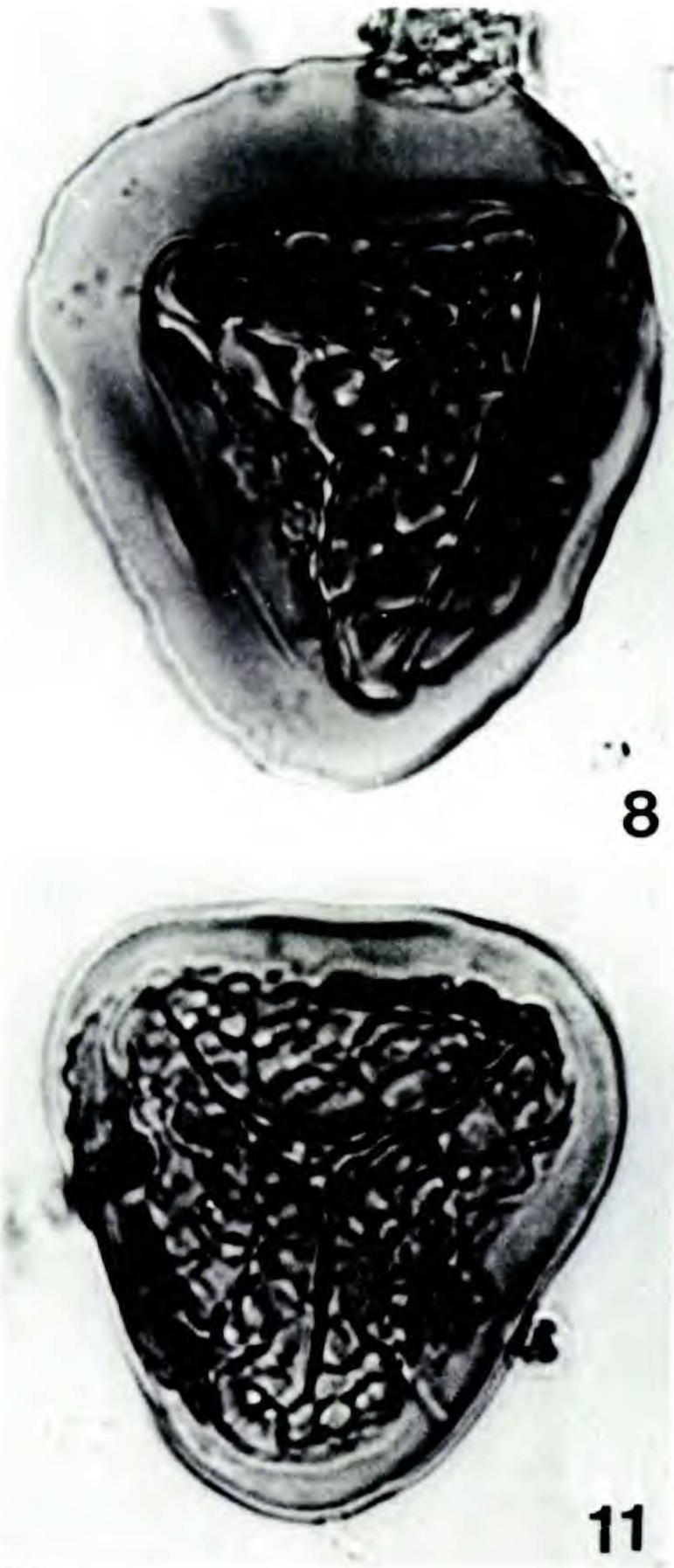
16-1, ESF L-33, 1–3.—5. *Lycopodium*, Pan A 21-1, ESF F-11, 3.—6. *Selaginella*, Pan A 16-3, ESF P-40, 3.—7. Trilete fern spore type 1, Pan A 16-2, ESF X-41, 1.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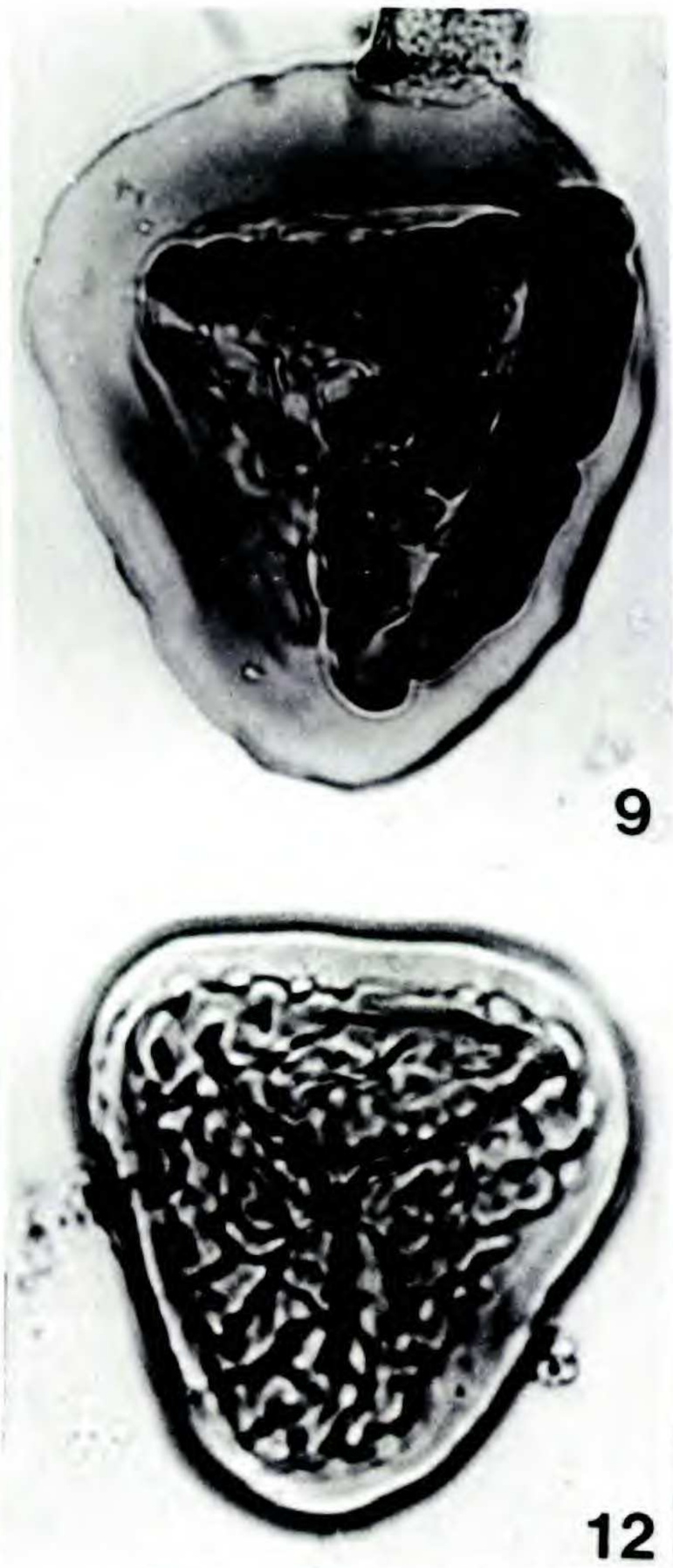
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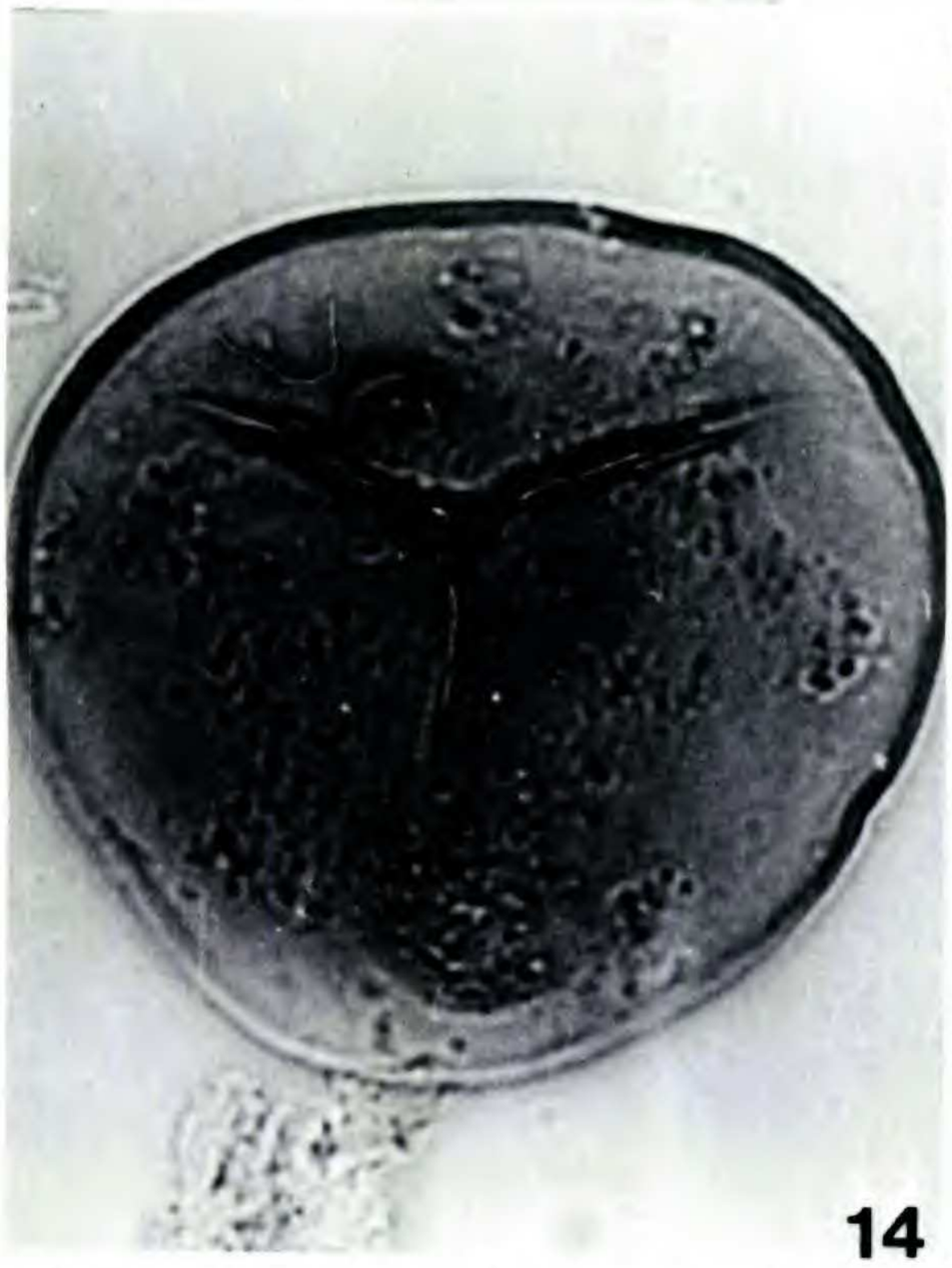
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FIGURES 8–17. Fossil spores from the La Boca Formation, Panama.—8, 9. *Pteris* type 1, Pan A 16-1, ESF S-35, 1.—10, 13. *Cyathea*, Pan A 16-1, ESF X-49; Pan A 16-2, ESF L-34.—11, 12. *Pteris* type 2, Pan A 16-2, ESF K-34.—14. Cf. *Antrophyum*, Pan B 50-2, ESF N-14, 2.—15. Trilete fern spore type 2, Pan B 30-3, ESF Q-46, 1–2.—16, 17. Trilete fern spore type 3, Pan A 21-1, ESF W-11, 1–3.

one genus. They are also known from the Uscari sequence of Costa Rica (Graham, 1987a, fig. 30).

Type 2 (Fig. 15). Amb oval-triangular to circular; trilete, laesurae straight, narrow, 17–20 μm long, extending ca. ¾ distance to spore margin, inner margin entire; finely reticulate; wall 1.5 μm thick; 45–48 μm.

Type 3 (Figs. 16, 17). Amb triangular, trilete, laesurae straight, narrow, 12–14 μm long, extending to or nearly to spore margin, prominent lip (partially folds?), inner margin entire; distal surface divided into low, irregular, verrucaelike segments by short, sinuous furrows, proximal surface more laevigate; wall 2–3 μm thick; 31–33 μm.

MONOLETE FERN SPORES

Reniform, monolete fern spores are common in all Tertiary formations studied for the Gulf/Caribbean region. They are produced by members of the Blechnaceae, Polypodiaceae, and Pteridaceae and range from Paleozoic to Recent. Five types illustrate the range in sculpture and size. Type 1 (Fig. 18; 45 × 32 μm) is laevigate; type 2 (Fig. 19; 70 × 46 μm) is finely verrucate; type 3 (Fig. 20; 69 × 51 μm) has numerous, small, densely arranged verrucae; type 4 (Fig. 21; 42 × 36 μm) is coarsely verrucate; and type 5 (Fig. 22; 54 × 36 μm) has prominent, widely scattered, peglike verrucae.

GRAMINEAE

Spherical, amb circular; monoporate, pore circular, 2 μm diam., inner margin entire, annulus ca. 2 μm wide, outer margin entire; tectate, wall ca. 2 μm thick; psilate to faintly scabrate; ca. 30 μm (folded) (Fig. 23).

The Gramineae are stenopalynous, and the specimens cannot be referred to any single genus. Grass pollen continues to be rare or absent in Gulf/Caribbean Tertiary deposits studied to date, with only a few grains previously reported from the Culebra and Paraje Solo formations. Specimens are known in the stratigraphic literature as *Monoporites annulatus* and range from the Paleocene (Brazil) to Recent (Muller, 1981, 1984).

PALMAE

Although several surveys of modern palm pollen are available (e.g., Ferguson, 1986; Thanikaimoni, 1970), it is still difficult to identify Gulf/Caribbean Tertiary specimens. The palms were a prominent component of the vegetation, and three types are recognized for the La Boca Formation.

Attalea type (Fig. 24). Wedge-shaped, with greatest diam. near pole; amb ca. rectangular; monocolpate, colpus straight, narrow, 19–22 μm long, inner margin entire to minutely dentate; scabrate; tectate, wall ca. 1.5 μm thick; 43–47 × 25–29 μm.

Attalea is a genus of about 40 species occurring in South America, the West Indies, and the Old World tropics, with one species (*A. allenii* H. Moore) listed for Panama (D'Arcy, 1987), where it grows at elevations up to ca. 1,000 m.

Manicaria type (Figs. 25–27). Prolate, with greatest diam. at or near equator; monocolpate, colpus straight to slightly sinuous, narrow, 30–42 μm long, extending nearly entire length of grain, inner margin entire; finely reticulate (diam. of lumen 1 μm or slightly less); tectate-perforate, wall ca. 1 μm thick; 36–48 × 21–30 μm.

Manicaria is a tree up to 10 m tall, with three species in the Antilles, Central America, and South America (fide Bailey, 1943), where it often occurs in dense groves in wet places. Similar pollen is known from the Gatuncillo and Culebra formations.

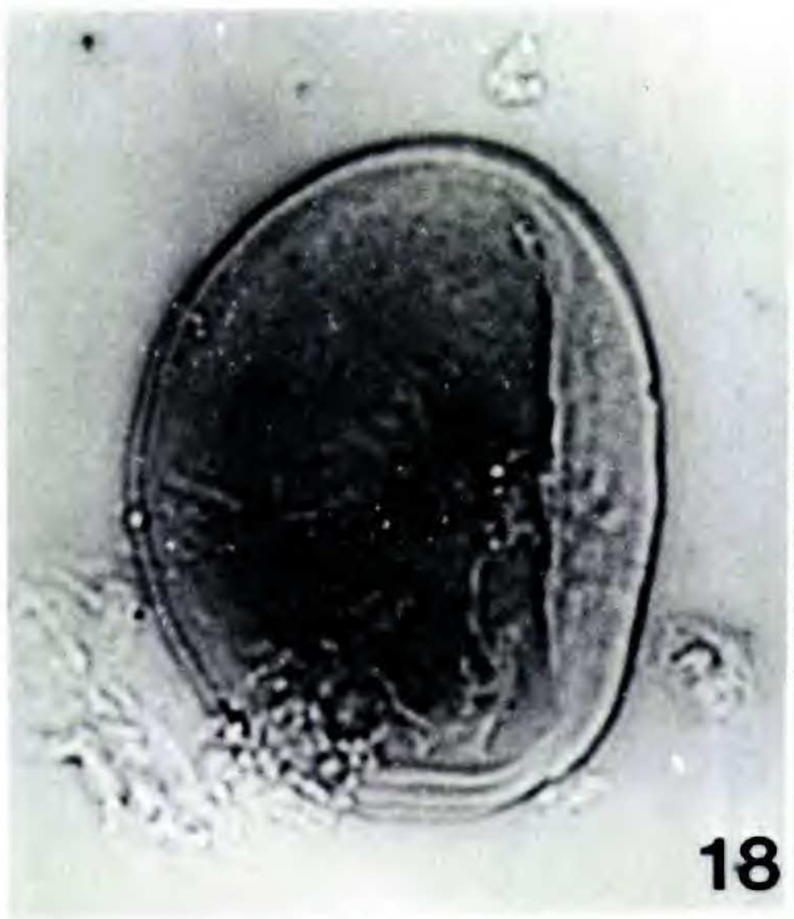
Synechanthus type (Figs. 28, 29). Prolate; monocolpate, colpus straight, narrow, 30–42 μm long, extending entire length of grain, inner margin entire; microreticulate; tectate-perforate, wall 1.5–2 μm thick; 36–48 × 30–38 μm.

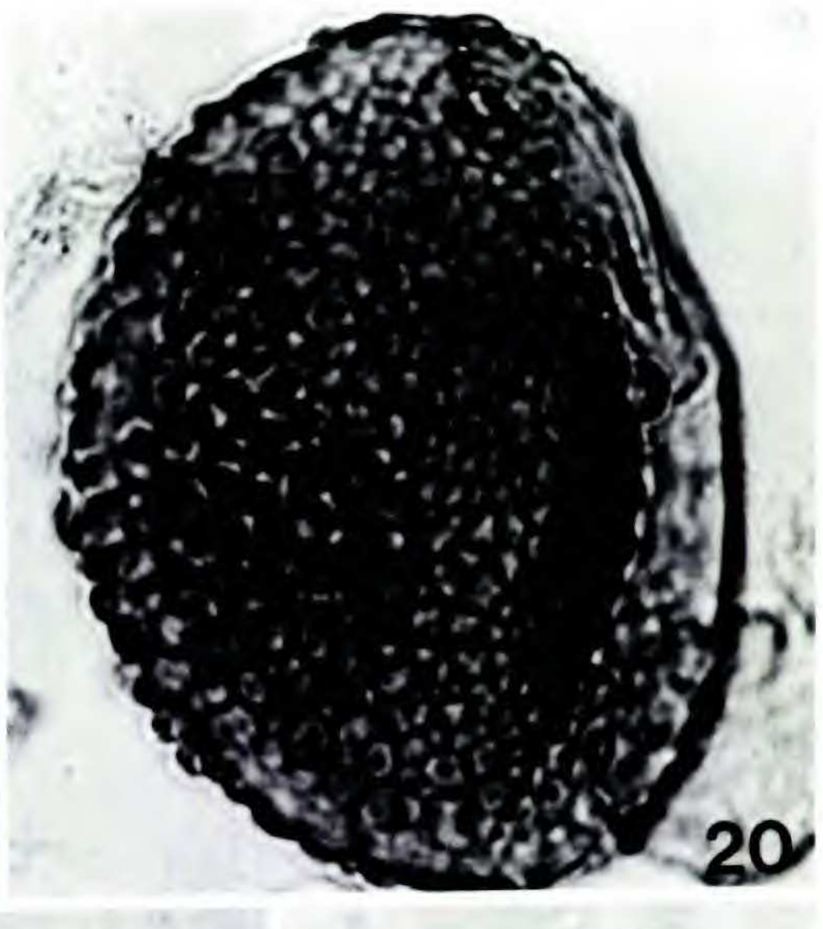
Synechanthus grows in Panama at low elevations in the tropical moist, premontane wet, and premontane rain forests (Croat, 1978: 178). Similar pollen occurs in the Culebra Formation.

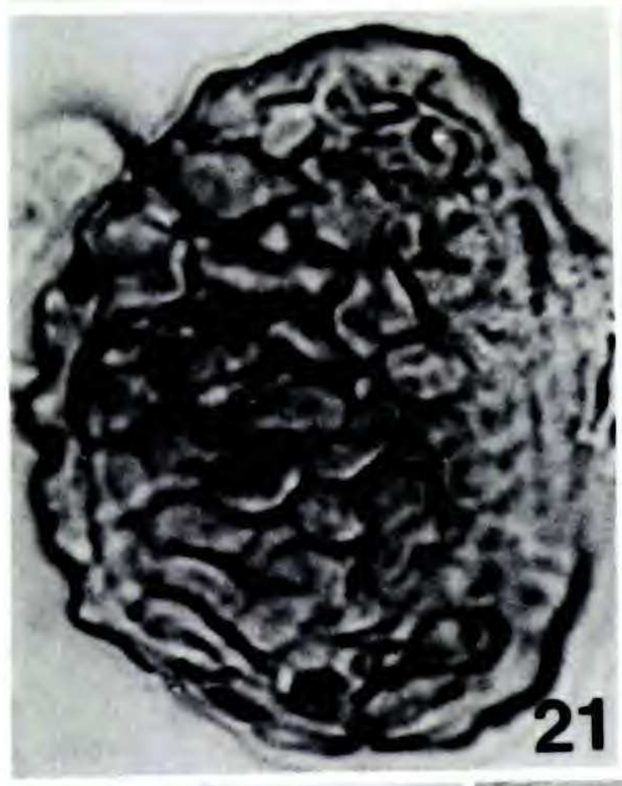
AQUIFOLIACEAE

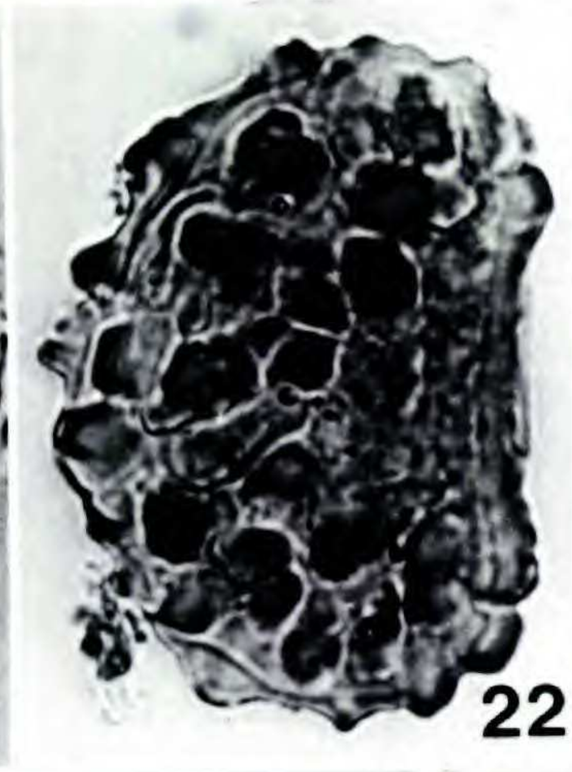
Ilex (Fig. 31). Oblate-spheroidal, amb oval to circular, tricolporoidate, colpi straight, 18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin diffuse, pores obscure, diam. ca. 2–3 μm, circular, situated at midpoint of colpus; intectate, clavate, wall 3 μm thick; 27 × 18 μm.

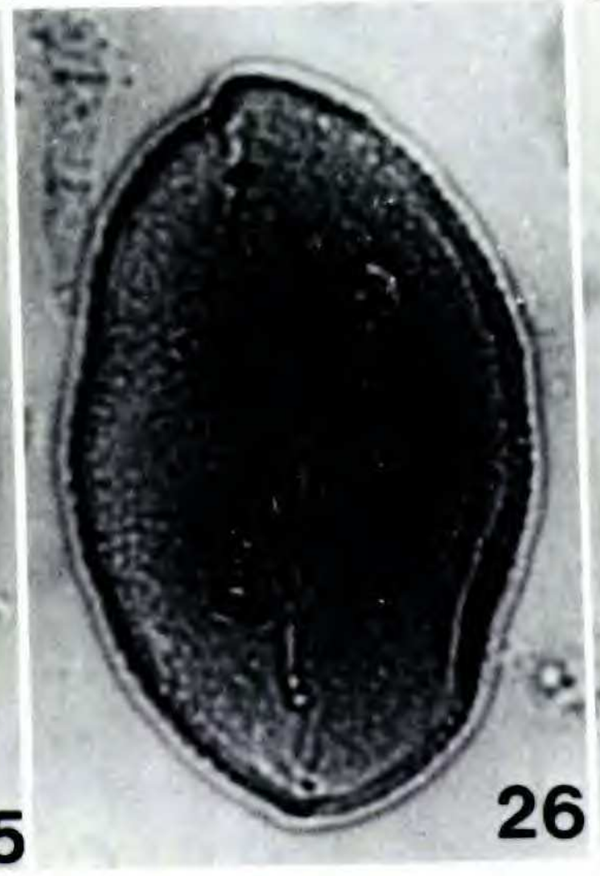
In Central America *Ilex* commonly grows at mid altitudes in moist to slightly drier habitats. It is a frequent component of Gulf/Caribbean Tertiary microfossil floras in low percentages and has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

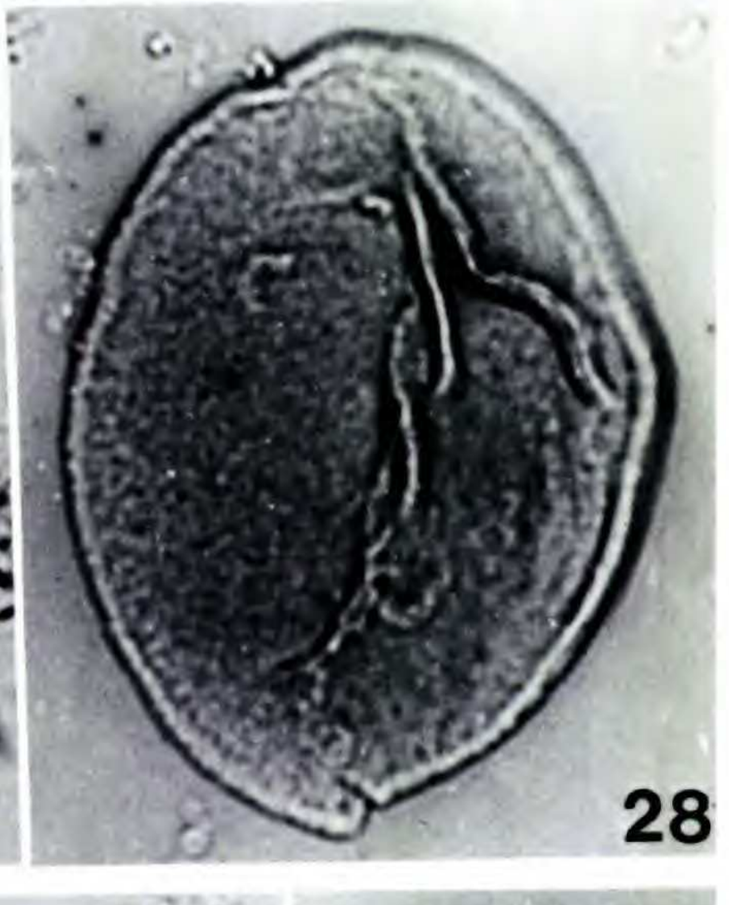


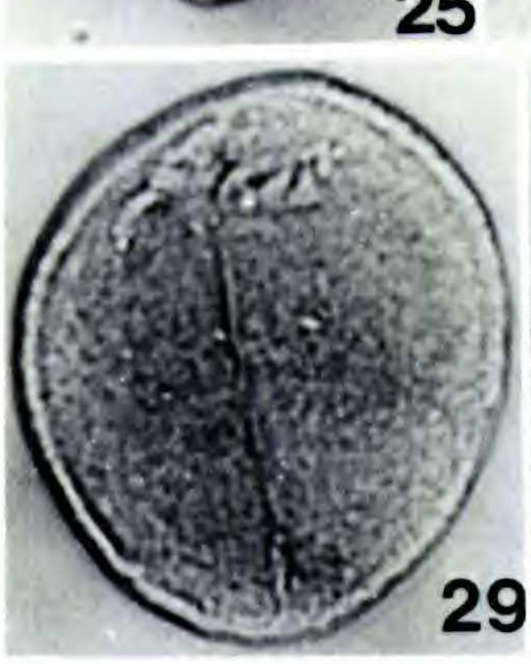


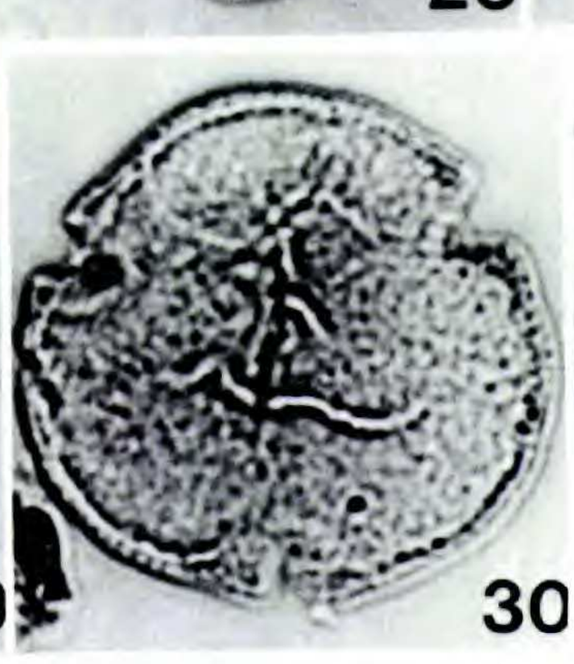


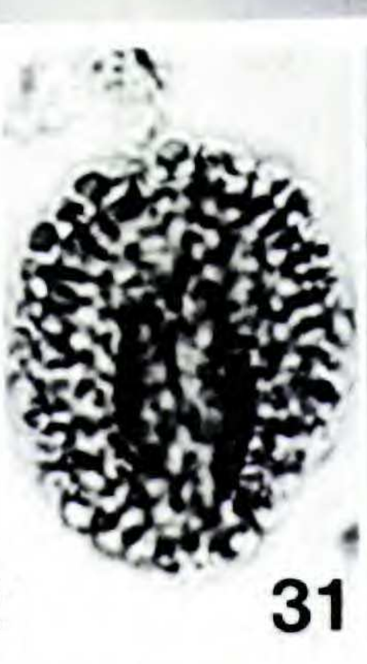












FIGURES 18–33. Fossil spores and pollen from the La Boca Formation, Panama.—18. Monolete fern spore type 1, Pan A 16-1, ESF D-32, 1–3.—19. Monolete fern spore type 2, Pan A 16-1, ESF T-45, 3.—20. Monolete fern spore type 3, Pan A 16-3, ESF J-43, 3–4.—21. Monolete fern spore type 4, Pan A 14-1a, ESF M-48, 3–4.—22. Monolete fern spore type 5, Pan B 50-2, ESF V-23, 1–2.—23. Gramineae, Pan A 14-1a, ESF W-35, 1.—24.

BOMBACACEAE

The pollen of several Bombacaceae are distinct (Tsukada, 1964; Nilsson & Robyns, 1986), but other generalized types cannot be referred to any one genus (see listings in Muller, 1981: 46–48). There is also some overlap with the closely related families Sterculiaceae and Tiliaceae, and in fossil deposits types are recovered that do not match exactly any extant members of the complex (Graham, 1976, figs. 248–255). It is possible that some unidentified pollen represents extant species not yet collected or extinct taxa from early speciation after introduction into the Caribbean region. Further studies are needed on the pollen morphology of modern forms, including newly described taxa, and a complete assessment should be made of fossil types.

Bombacaceae are prominent members of neotropical forests, and the pollen is frequent but not abundant in Tertiary sediments. Muller (1981: 46–48) listed the oldest occurrence of this family as Maestrichtian (uppermost Cretaceous) from the southeastern United States and cited other records supporting Wolfe's (1975) suggestion that the family originated in eastern North America and subsequently spread to South America and Africa where it diversified. In the Caribbean region it first appears in the Paleocene of northern South America (*Bombacacidites annae* = *Bombax ceiba* type; Germeraad et al., 1968: 277), and in our material, pollen of the family occurs in the San Sebastian Formation and Uscari sequence.

Cf. Aguiaria (Fig. 30; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 7f, g). Oblate, amb circular; tricolpate, colpi short (8–10 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin minutely dentate, bordered by narrow margo ca. 1.5–2 μm wide; finely reticulate; tectate-perforate, wall ca. 2 μm thick; 30–34 μm.

Cf. Ceiba (Fig. 34; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 11I). Oblate, amb circular; tricolpate, colpi short (13–15 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire to minutely dentate, bordered by narrow margo ca. 2–3 μm wide; reticulate, muri smooth, slightly sinuous, narrow (ca. 0.5–1 μm), lumina polygonal, 4–5 μm diam. at poles, smaller toward equator; tectate-perforate, wall ca. 1.5 μm thick; 56–60 μm.

Pseudobombax (Fig. 35; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 6I). Oblate, amb triangular, sides slightly concave, apices rounded; tricolpate, colpi short (8–10 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire, bordered by faint narrow margo ca. 1 μm wide; reticulate at poles, muri smooth, straight to occasionally curved, narrow (ca. 1 μm), lumina polygonal, ca. 3 μm diam., becoming minutely reticulate around apices; tectate-perforate, wall 1.5–2 μm thick; 54–56 μm.

Pseudobombax is a tree to 25 m tall distributed from Nicaragua to Brazil and Peru. In Panama it typically occurs at lower elevations in the tropical moist forest but is also found in the premontane moist, tropical wet, and locally from the tropical dry forest (Croat, 1978: 591).

EUPHORBIACEAE

Alchornea (Fig. 32). Oblate, amb circular; tricolpate, colpi straight, 6–8 μm long (apex to equator), equatorially arranged, meridionally elongated, equidistant, extending within 6–7 μm of pole, inner margin entire, operculum distinct; psilate to faintly scabrate; tectate, wall 1.5 μm thick; 18–20 μm.

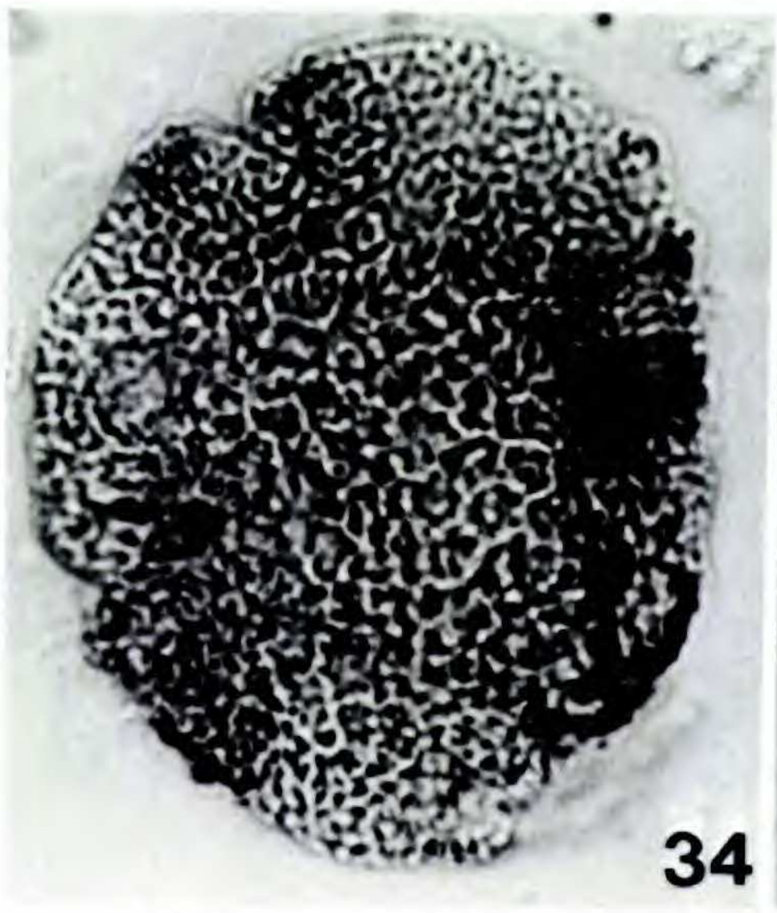
Pollen of *Alchornea* is frequent in low numbers in Gulf/Caribbean Tertiary deposits. It ranges from the lower and middle Eocene (Colombia; González Guzmán, 1967) to Recent (Muller, 1981). Its ecology and distribution have been summarized by Graham (1987a) based on Croat (1978) and Webster & Burch (1967). In Central America *Alchornea* grows in the tropical moist, premontane wet, and premontane rain forest typically at elevations between 300 and 2,000 m.

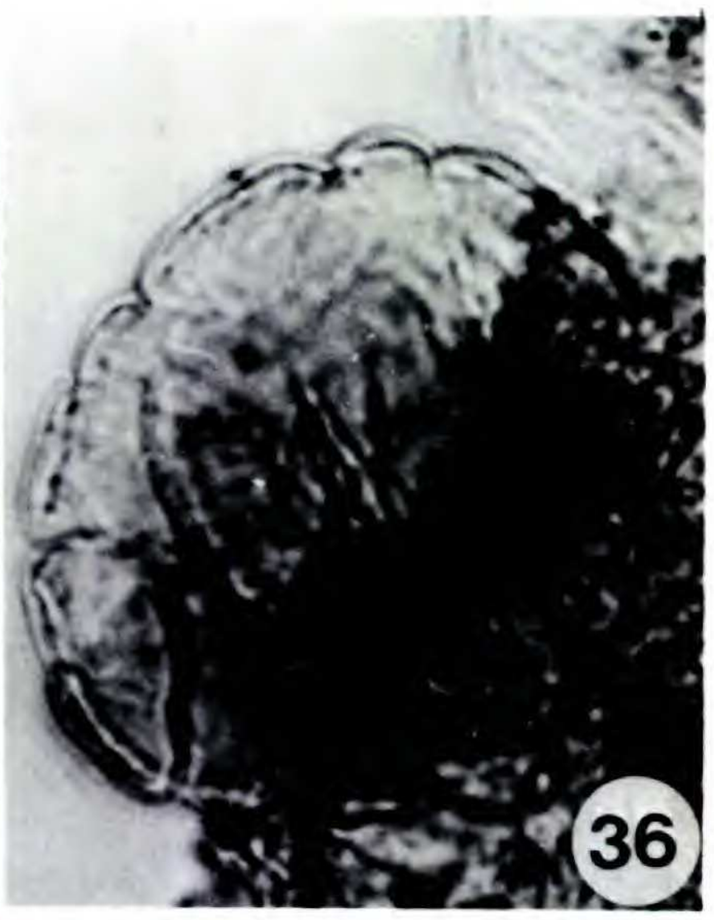
JUGLANDACEAE

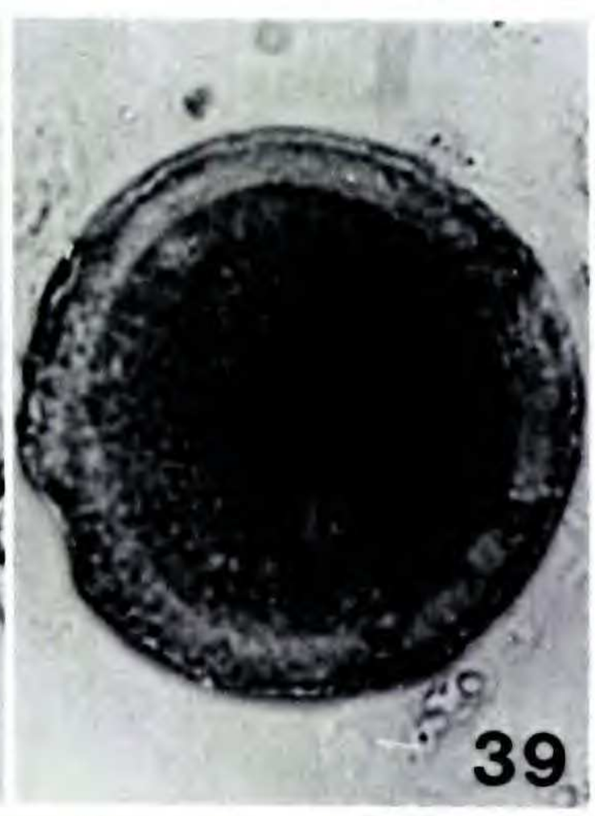
Alfaroa/Engelhardia (Fig. 33). Oblate, amb oval-triangular; triporate, pores circular, ca. 2 μm diam., inner margin entire, equatorially arranged, equidistant; psilate; tectate, wall 1.5–2 μm thick; 20–25 μm.

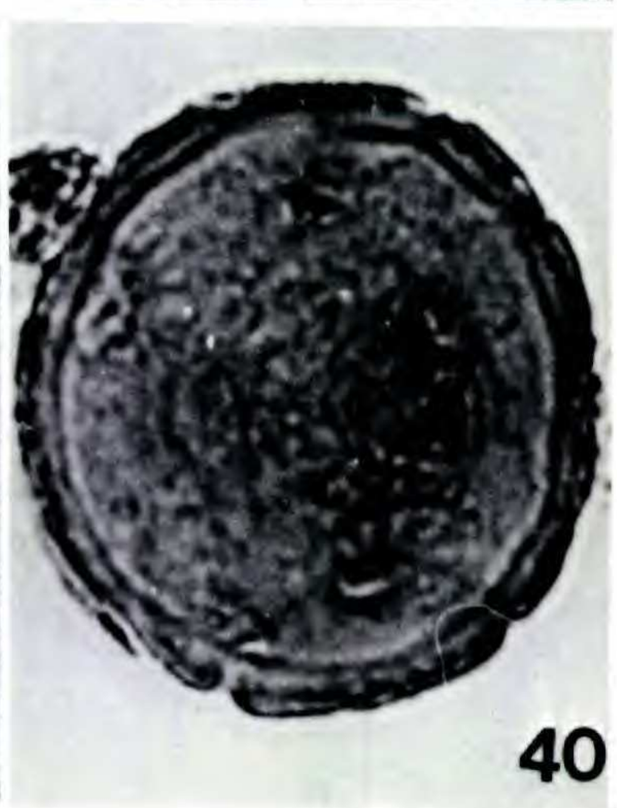
←

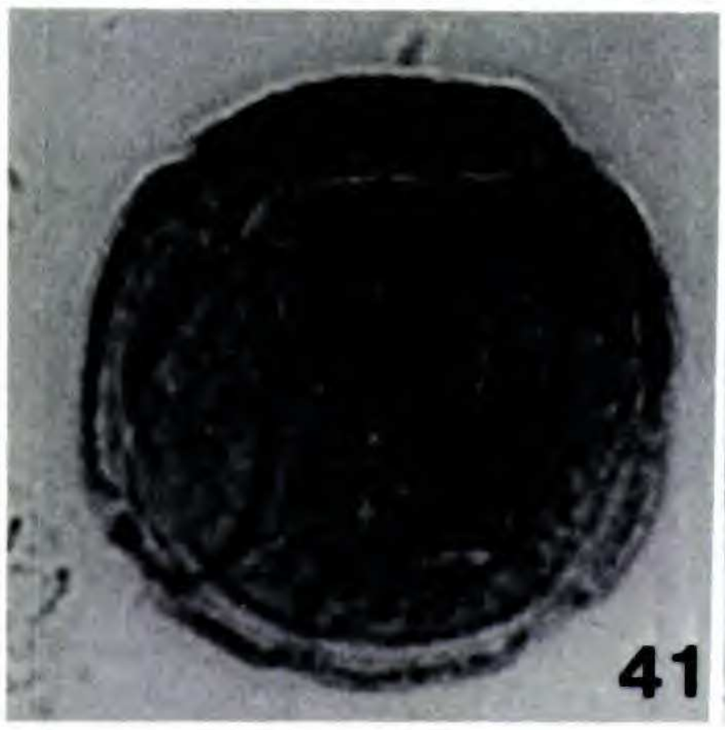
Attalea type, Pan A 16-2, ESF U-38, 2.—25–27. *Manicaria* type, Pan A 14-1a, ESF U-34, 1–3; Pan A 20-2, ESF Y-22, 2–4; Pan A 20-2, ESF G-19, 4.—28, 29. *Synechanthus* type, Pan A 16-1, ESF D-44, 1–3; Pan A 16-1, ESF L-46, 1–3.—30. Cf. *Aguiaria*, Pan A 16-2, ESF D-42.—31. *Ilex*, Pan A 16-3, ESF K-46.—32. *Alchornea*, Pan A 16-3, ESF E-33, 2.—33. *Engelhardia*, Pan A 20-2, ESF T-43, 4.

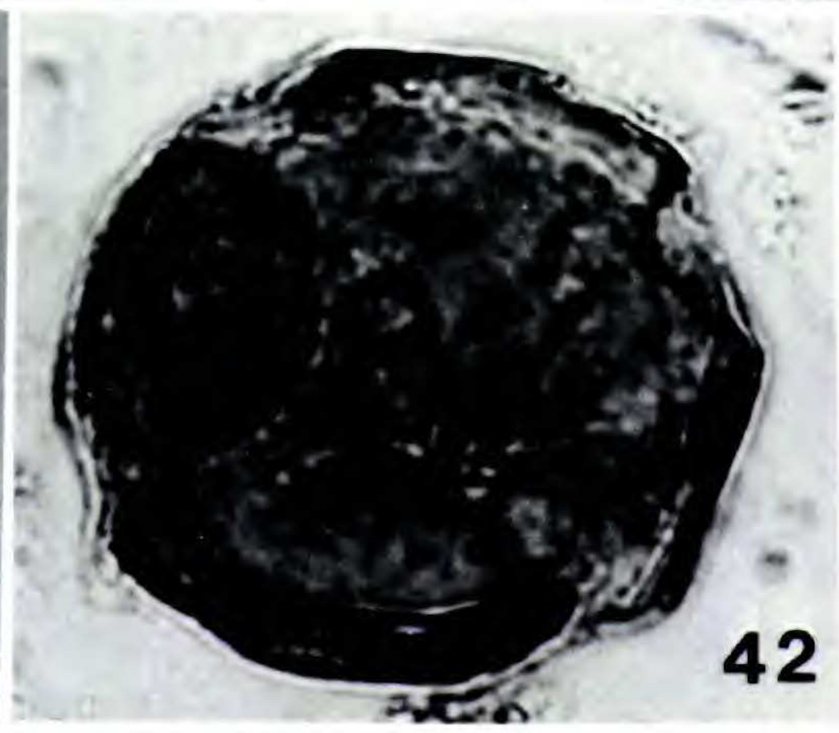


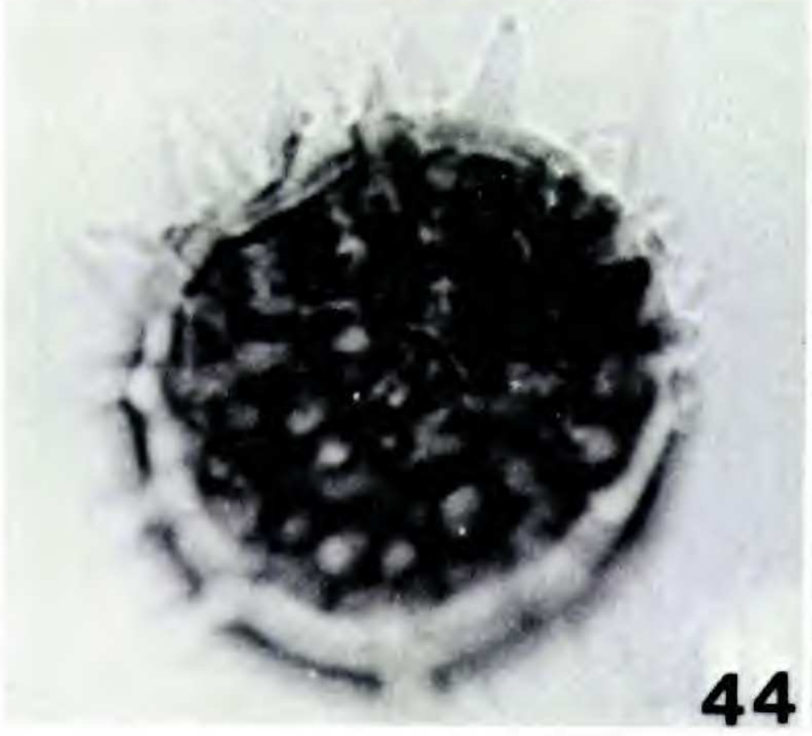


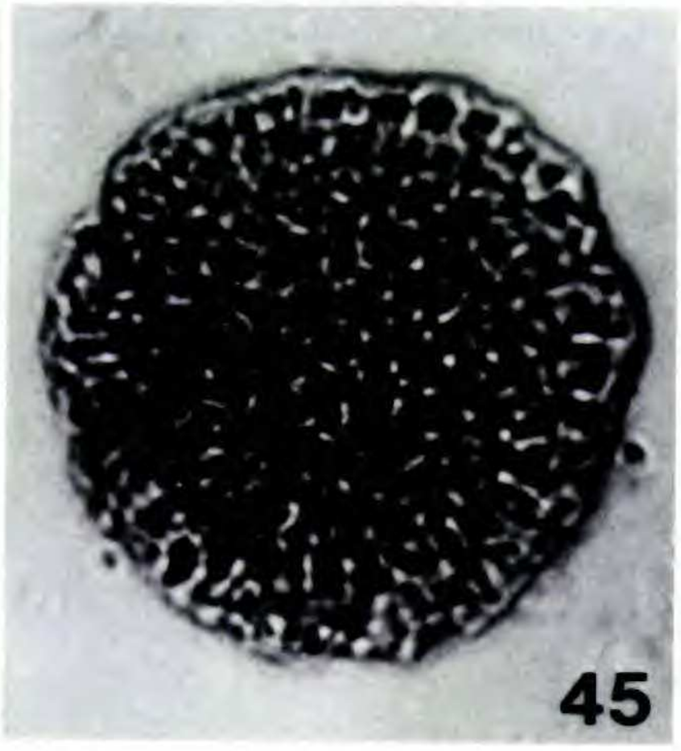


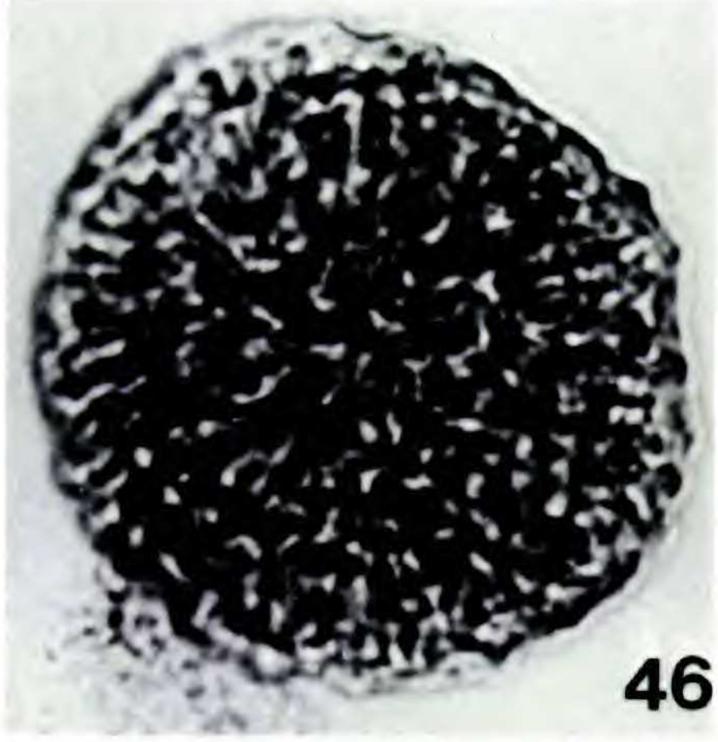












FIGURES 34–46. Fossil pollen from the La Boca Formation, Panama.—34. Cf. *Ceiba*, Pan A 16-2, ESF O-31, 2–4.—35. *Pseudobombax*, Pan A 20-2, ESF N-36, 3–4.—36. *Utricularia*, Pan A 14-1a, ESF V-32.—37, 38. *Crudia*, Pan A 16-3, ESF X-31; Pan A 16-1, ESF X-47, 1–3.—39. Malpighiaceae type 1, Pan A 16-3, ESF W-39, 2.—40. Malpighiaceae type 2, Pan B 50-2, ESF L-36, 1–2.—41. Malpighiaceae type 3, Pan B 50-2, ESF

These trees are distributed from Mexico through Central America, usually associated with lower- to mid-altitude temperate forests. Pollen occurs in the Gatuncillo, San Sebastian, Cucaracha, and Paraje Solo formations.

LEGUMINOSAE—CAESALPINIOIDEAE

Crudia (Fig. 37, 38). Prolate; tricolporoidate, colpi narrow, straight, 25 μm long, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, circular, situated at midpoint of colpus; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine; tectate but with occasional separation between sculpture elements, wall 1.5 μm thick; 42–48 × 30–32 μm.

Crudia is a South American, mainly Amazonian, riverine tree of low altitudes (Cowan & Polhill, 1981: 131). Pollen ranges from the Eocene in northern South America (as *Striatocolpites catumbus*) and from the Paleocene in Africa (Muller, 1981). It occurs in Central America in the Gatuncillo and Cucaracha formations. Modern pollen has been studied by Graham & Barker (1981).

LENTIBULARIACEAE

Utricularia (Fig. 36). Oblate, amb circular; stephanocolpate, colpi 12–16, equatorially arranged, meridionally elongated, equidistant, 15–18 μm long, extending within 8–10 μm of pole, inner margin entire; psilate to faintly scabrate; tectate, wall 2 μm thick; 34–36 μm.

Utricularia is an annual or stoloniferous perennial, insectivorous, aquatic herb growing along the margins of freshwater lakes and rivers, swamps, and marshes from Florida to Mexico and south through the Antilles, Central America, and South America. It is represented by about 12 species in Panama (Taylor, 1976). Pollen also occurs in the Paraje Solo Formation.

MALPIGHIACEAE

Representation of the Malpighiaceae in the Gulf/Caribbean Tertiary is analogous to the Bombacaceae, wherein several types are present but many do not match exactly modern reference material or species illustrated in the literature. Generally similar modern forms include *Banisteria*, *Banisteriopsis*, *Bunchosia*, *Hiraea*, *Malpighia*, and *Mascagnia*; but since the specimens are slightly different, they are referred to types 1–5.

Type 1 (Fig. 39). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire; scabrate; tectate, wall 5–6 μm thick; 42 μm.

The distinguishing features of this grain are the very thick wall and the absence of colpi connecting the pores.

Type 2 (Fig. 40). Spherical, amb circular; periporate, pores circular, 3 μm diam., inner margin entire, faint colpi with diffuse, granular margins connecting the pores; scabrate; tectate, wall 2 μm thick; 35 μm.

These specimens have moderately thick walls and faint connecting colpi.

Type 3 (Fig. 41). Spherical, amb circular; periporate, pores circular, 1.5–2 μm diam., inner margin entire, colpi with diffuse, granular margins connecting the pores; scabrate, some scabrae pointed; tectate, wall 2 μm thick; 36 μm.

The distinguishing features of type 3 are the moderately thick wall, distinct colpi, and some scabrae with pointed apices.

Type 4 (Fig. 42). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire, colpi with diffuse granular margins connecting the pores; scabrate; tectate, wall 5 μm thick; 45 μm.

These specimens differ from the thick-walled type 1 by having distinct colpi.

Type 5 (Fig. 43). Spherical, amb circular; periporate, pores circular, 1.5 μm diam., colpi with diffuse granular margins connecting the pores, colpi and pores numerous, giving scalloped appearance to outer margin of grain; psilate; tectate, wall 5–6 μm thick; 37 μm.

These thick-walled specimens have numerous pores and colpi, and they are psilate.

MALVACEAE

Spherical, amb circular; apertures obscure, periporate(?), pores circular, small (ca. 1.5 μm), evenly

←

E-27, 2–4.—42. Malpighiaceae type 4, Pan A 16-3, ESF P-43, 2–4.—43. Malpighiaceae type 5, Pan A 16-3, ESF O-43, 1.—44. Malvaceae, Pan A 21-1, ESF R-21, 2–4.—45. Rubiaceae type 1, Pan A 20-2, ESF W-20, 1–2.—46. Rubiaceae type 2, Pan A 20-2, ESF L-31, 1.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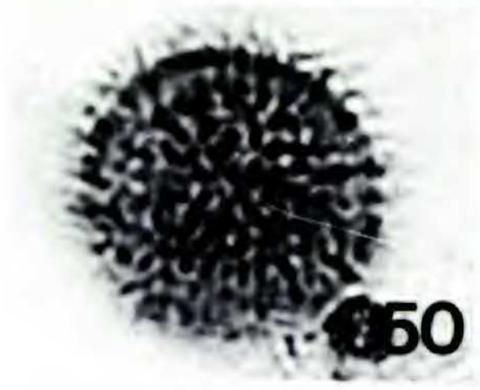
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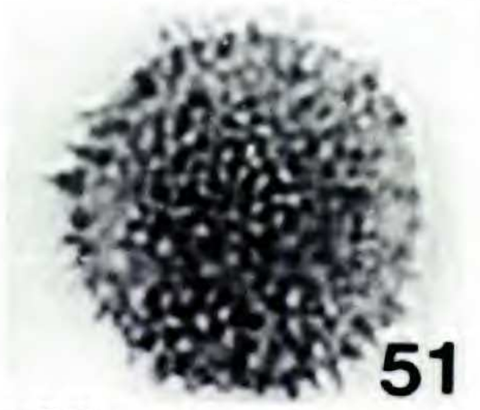
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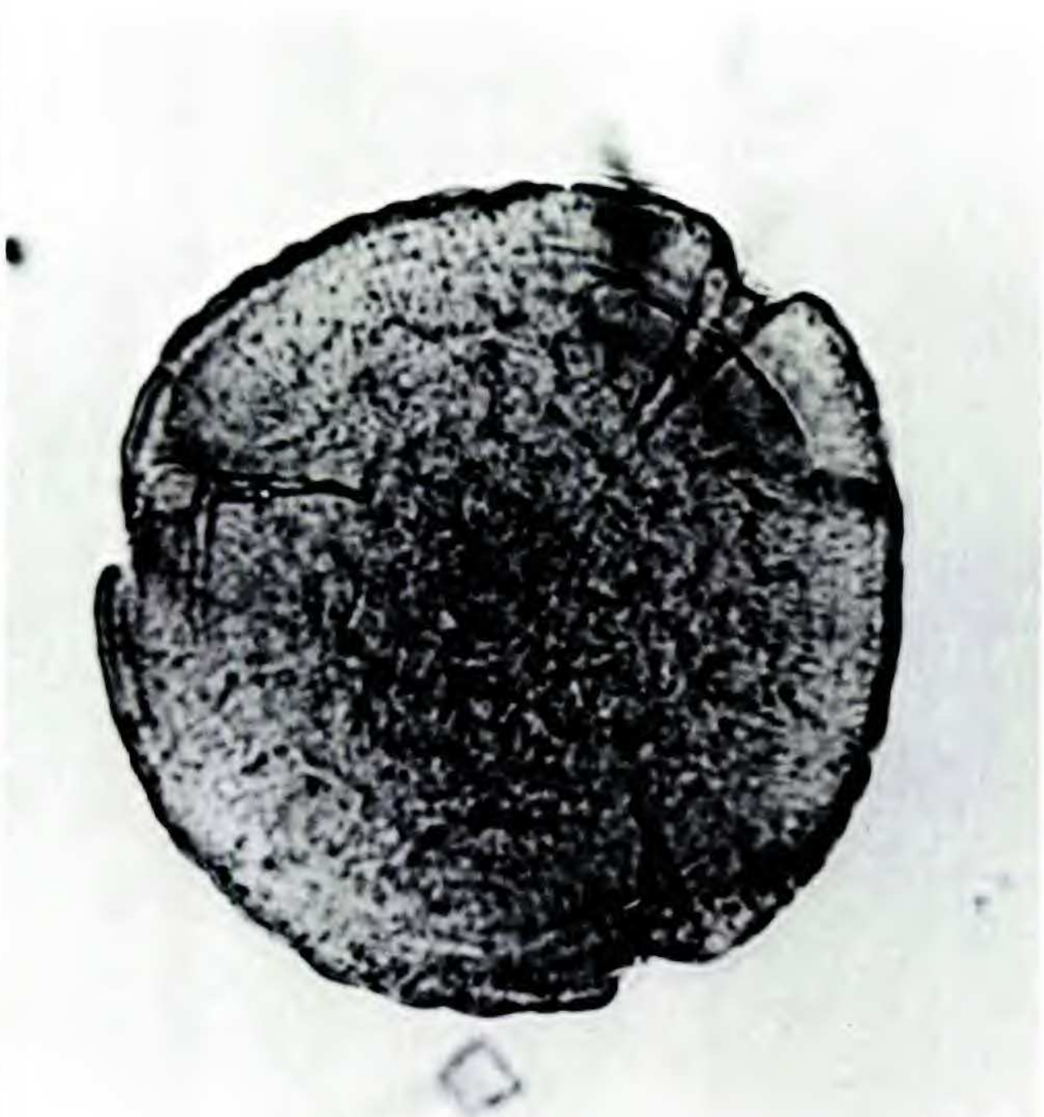
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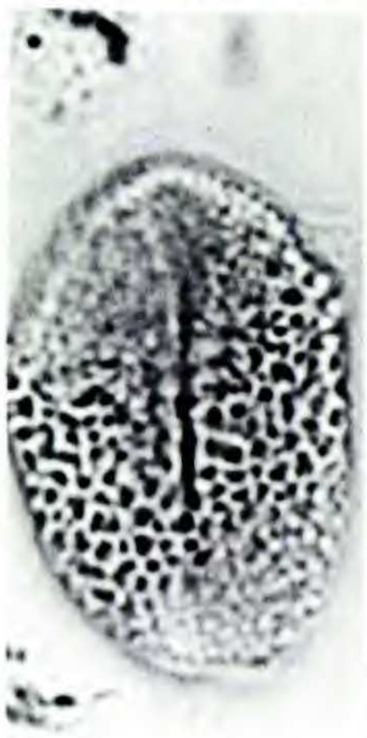
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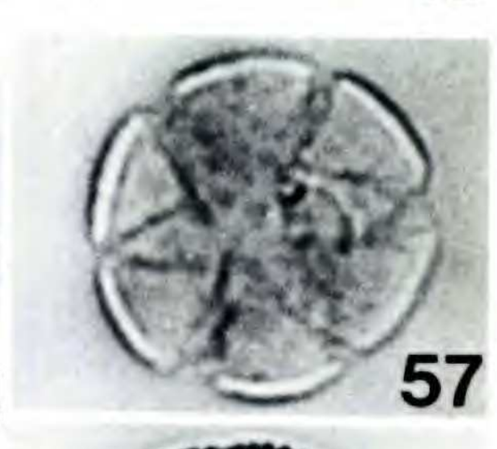
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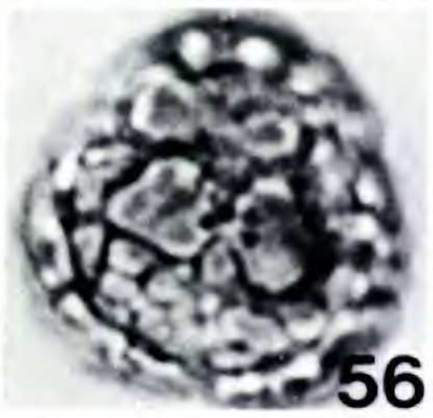
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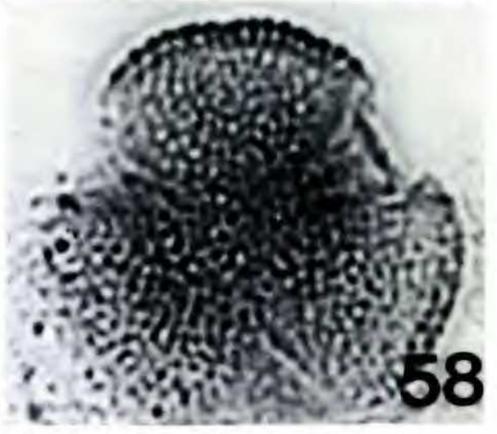
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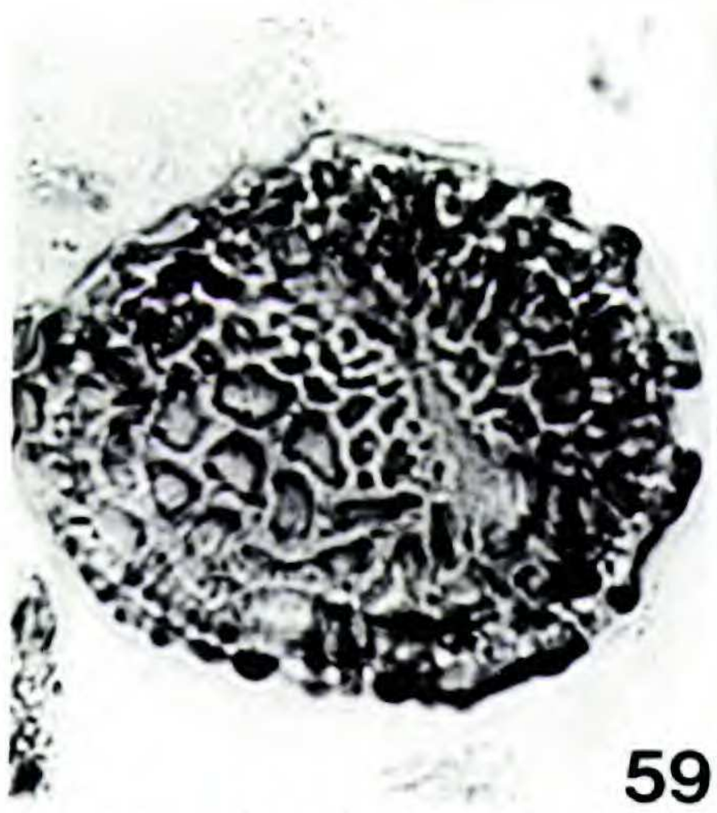
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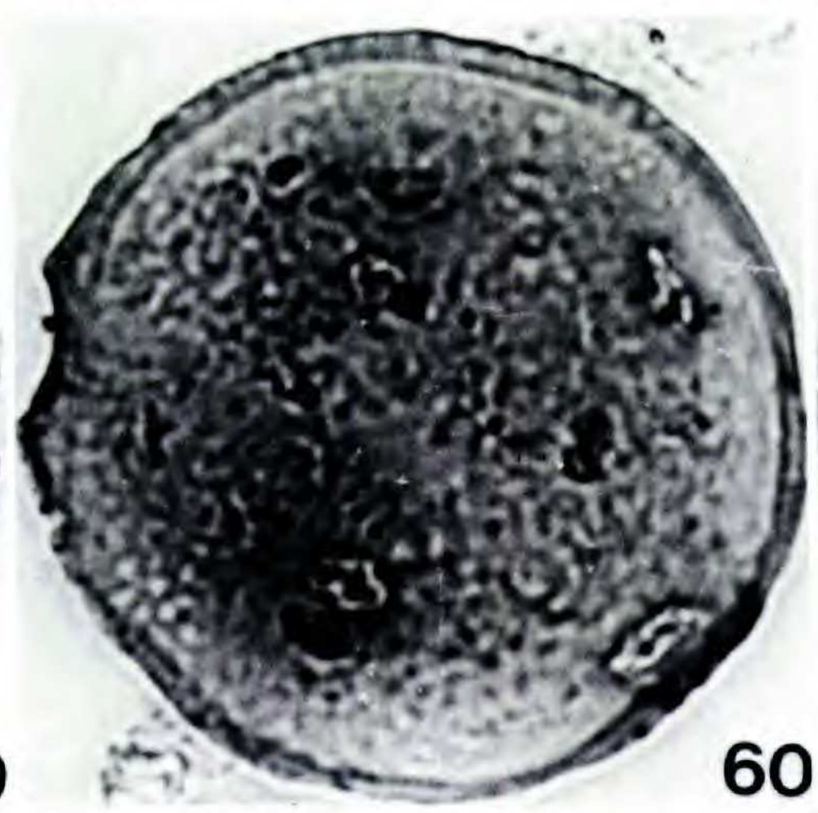
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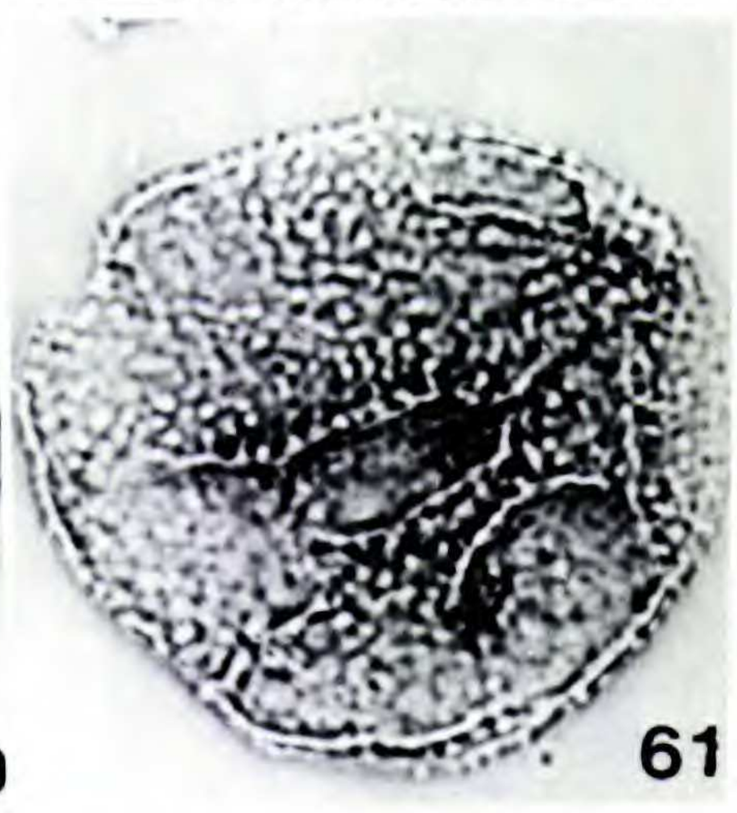
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FIGURES 47–61. Fossil pollen from the La Boca Formation, Panama.—47. *Rhizophora*, Pan B-50, 2, ESF X-33, 2.—48, 49. *Pelliciera*, Pan A 5-2, ESF N-39, 1–2; Pan A 16-3, ESF V-44, 3–4.—50. Unknown 1, Pan A 20-2, ESF E-26.—51. Unknown 2, Pan B 50-2, ESF N-11, 4.—52. Unknown 3, Pan A 16-2, ESF 32, 3–4.—53. Unknown 4, Pan A 14-1a, ESF N-45, 1–3.—54. Unknown 5, Pan A 16-2, ESF T-28, 2.—55, 56. Unknown 6, Pan A 14-1a, ESF Q-30.—57. Unknown 10, Pan A 14-1a, ESF G-29, 2–4.—58. Unknown 11, Pan B 50-2, ESF V-13, 3–4.—59. Unknown 7, Pan A 16-3, ESF Q-47, 2.—60. Unknown 8, Pan B 50-2, ESF F-33, 2.—61. Unknown 9, Pan A 16-1, ESF G-45.

distributed, inner margins entire; echinate, echinae hyaline, straight, broad at the base, densely arranged, 5 μm long, decreasing to 2–3 μm on portions of the exine; psilate; tectate, wall 1.5–2 μm thick; 30 μm (Fig. 44).

This unusual specimen may be an aberrant form and cannot be identified to genus. The Malvaceae are represented in the Caribbean Tertiary by *Hampea/Hibiscus* (probably *Hibiscus tiliaceus* L.) in the Culebra Formation and are frequent in the Tertiary of northern South America (as *Echiperiporites estelae*, late Eocene to Recent).

RHIZOPHORACEAE

Rhizophora (Fig. 47). Prolate to prolate-spheroidal; tricolporate, colpi straight, 14–16 μm, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 2–3 μm wide, pores elongated equatorially (colpi transversalis), 1 × 4 μm, constricted at midpoint of colpus; finely reticulate; tectate-perforate, wall 2–3 μm thick; 16–20 × 14–18 μm.

Pollen of *Rhizophora* has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations and comprises 90% or more of some samples. Its fossil record has been discussed by Langenheim et al. (1967), Leopold (1969), and Muller & Caratini (1977), and its occurrence in the Gulf/Caribbean Tertiary was summarized by Graham (1985: 519, 1987a). *Rhizophora* is indicative of coastal, brackish-water conditions in tropical to subtropical regions. It is known in the stratigraphic literature as *Zonocostites ramonae* and ranges from the late Eocene to Recent. In older Tertiary deposits in Latin America it is replaced by its presumed ecological equivalent *Brevitricolpites* of unknown biological affinity.

RUBIACEAE

The Rubiaceae are represented in the La Boca Formation by two similar pollen types typical of several extant genera. These tricolpate, densely sculptured forms are produced by *Anisomeris*, *Chomelia*, *Guettarda*, *Terebraria*, and others.

Type 1 (Fig. 45). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (4–5 μm apex to equator), often obscured by dense sculpture; reticulate, muri 1.5 μm wide, smooth, straight to occasionally curved or slightly sinuous, lumina 2–3 μm diam.; tectate-perforate, wall 2 μm thick; 26–36 μm.

Type 2 (Fig. 46). Similar to type 1 but is slightly larger (42–46 μm), and the muri are thicker (ca. 2–2.5 μm).

THEACEAE

Pelliciera (Figs. 48, 49). Oblate, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, 20–26 μm, tapering to acute apex, inner margin entire, pore circular, 3–4 μm diam., situated at midpoint of colpus, inner margin entire; sculpture variable from finely to coarsely verrucate; tectate, wall 4 μm diam.; size variable, 40–60 μm.

Pelliciera is a small mangrove tree of lowland coastal areas from Costa Rica to northwest Colombia and Ecuador. In the Tertiary, however, it was widespread in the Gulf/Caribbean and is known from the lower middle Eocene Yellow Limestone Group of Jamaica, the middle(?) to late Eocene Gatuncillo Formation of Panama, the middle to late Oligocene San Sebastian Formation of Puerto Rico, the Oligo-Miocene Simojovel Group of Mexico, and from several localities in northern South America. Several anther-size clusters or fragments (Fig. 49) were recovered, indicating the plants grew in the immediate vicinity of the depositional basin. The presence of *Pelliciera* pollen in the La Boca Formation is one of the principal differences between that unit and the Culebra and Cucaracha formations. In the stratigraphic record it is known as *Psilatricolporites crassus* and ranges from the Eocene to Recent. Other details of the ecology and geologic record of *Pelliciera* have been summarized by Graham (1977).

UNKNOWNS

A number of specimens were recovered that could not be identified. Some of the more distinctive and/or abundant ones are illustrated and briefly described below.

Unknown 1 (Fig. 50). Spherical, amb circular; apertures obscure (nonaperturate?); echinate, echinae straight to slightly curved, dense, 2–3 μm long; wall 1.5 μm thick; 16 μm.

Unknown 2 (Fig. 51). This type is similar to unknown 1 but is slightly larger (22 μm), and the spines are shorter (1 μm) and blunt.

Unknown 3 (Fig. 52). Prolate, amb oval; monocolpate, colpus straight, 22 μm long, inner margin minutely dentate; reticulate, muri straight, smooth, 1.5 μm wide, lumina 1–1.5 μm diam., reticulum

becoming finer toward poles; tectate-perforate, wall 2 μm thick; 36 × 27 μm.

These monocot pollen grains may be palms but no exact match has been found.

Unknown 4 (Fig. 53). Prolate, amb oval; monocolpate, colpi straight, 28 μm long; reticulate, reticulum deep (columellae 3 μm long), muri straight, smooth, 1 μm wide, lumina 2 μm diam.; tectate-perforate, wall 3–4 μm thick; 40 × 30 μm.

Unknown 5 (Fig. 54). Prolate, amb oval; monocolpate, colpus 42 μm long, extending entire length of grain, inner margin entire; echinate, echinae straight, 1.5 μm long, moderately dense; tectate, wall 1–1.5 μm thick; 45 × 24 μm.

Unknown 6 (Figs. 55, 56). Oblate-spheroidal, amb circular; tricolpate, colpi often obscured by coarse sculpture elements, short (5–6 μm long), equatorially arranged, meridionally elongated, equidistant; coarsely verrucate; tectate, wall 3 μm thick; 22–26 μm. Similar specimens occur in the Paraje Solo Formation.

Unknown 7 (Fig. 59). Oblate-spheroidal, amb circular; tricolpate, colpi straight, 15 μm long, inner margin lobate; reticulate, muri straight, smooth, 2 μm wide, lumina polygonal, 4 μm diam., becoming finer toward colpi forming a margo, reticulum deep (columellae 5 μm long); tectate-perforate, wall 6 μm thick; 45 μm.

Unknown 8 (Fig. 60). Spherical, amb circular; periporate, pores circular, 3 μm diam., widely spaced, inner margin entire; scabrate; tectate, wall 2 μm thick; 43 μm.

Unknown 9 (Fig. 61). Oblate, amb oval-triangular; tricolpate, colpi short (4 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin minutely dentate; echinate, echinae short (0.5 μm), moderately dense, bases forming subreticulum; tectate, wall 1 μm thick; 40 μm.

Unknown 10 (Fig. 57). Oblate-spheroidal, amb circular; stephanocolpate, colpi 6, straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire; scabrate; tectate, wall 1 μm thick; 16–21 μm.

Similar specimens occur in the Culebra Formation.

Unknown 11 (Fig. 58). Oblate-spheroidal, amb circular; tricolpate, colpi straight, tapering to acute apex, 6–8 μm long, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; finely reticulate; tectate-perforate, wall 2 μm thick; 27 μm.

Unknown 12 (Fig. 62). Prolate, amb oval; tricolporate, colpi straight, 45 μm long, equatorially arranged, meridionally elongated, equidistant, bordered by costae colpi 4–5 μm wide, inner margin entire, pores large, oval, 5 × 16 μm, situated at midpoint of colpus, inner margin entire; reticulate; tectate-perforate, columellae relatively coarse and clearly evident in median optical section, wall 2.5–3 μm thick; 58 × 36 μm.

Unknowns 12–15 are similar to pollen of several Anacardiaceae and Euphorbiaceae but cannot be referred to any one modern genus.

Unknown 13 (Fig. 63). This type is similar to unknown 12, but the columellae are shorter and finer; consequently, the wall is thinner (1.5–2 μm) and the reticulum finer.

Unknown 14 (Fig. 64). This type has an even thinner wall (1–1.5 μm), a finer reticulum, narrower costae colpi, and smaller and slitlike pores (2 × 4 μm).

Unknown 15 (Fig. 65). This type is similar to unknown 14 but is smaller (27–32 × 18–21 μm).

Paleocommunities and Paleoenvironments

Results of the La Boca study are of interest in demonstrating an internal consistency in paleocommunities, climates, and physiography among four fossil floras in two countries of Central America, as well as consistency with independent plate tectonic and paleotemperature data. The lower Miocene Uscari (Costa Rica), Culebra, Cucaracha, and La Boca (Panama) floras preserve elements of a mangrove swamp (*Pelliciera*, *Rhizophora*) fringing the volcanic islands constituting the isthmian region during most of the Tertiary. Freshwater marshes and swamps (palms, ferns, *Utricularia*) occupied lowland areas behind the mangrove zone. On the adjacent slopes were versions of the tropical wet, tropical moist, and premontane forests (*Lycopodium*, *Selaginella*, *Cyathea*, *Pteris*, *Ilex*, *Pseudobombax*, *Alchornea*, and *Crudia*, with *Alfaroa/Engelhardia* likely occupying distant, moderate highlands in the region). All available paleobotanical data are consistent in showing little evidence of dry (including savannah) habitats. Grass pollen continues to be poorly represented (maximum of 1% in one sample from the Culebra Formation; less than 0.5% in two samples from the La Boca) to absent (Uscaria, Cucaracha formations). If savannahs existed, as suggested by the

FIGURES 62–65. Fossil pollen from the La Boca Formation, Panama.—62. Unknown 12, Pan A 21-1, ESF X-14, 3.—63. Unknown 13, Pan A 16-1, ESF Q-44, 1–3.—64. Unknown 14, Pan A 16-3, ESF W-33, 4.—65. Unknown 15, Pan A 16-2, ESF W-36, 2–4.

grazing and browsing components of the Tertiary faunas, they were probably short-lived and developed locally as recovery vegetation in response to volcanic activity documented for central Panama in the form of extensive ash, tuff, and basalt deposits (see further discussion in Graham, 1988b). The affinities of the La Boca flora are clearly with Central America and areas to the north, reflecting the establishment of a land connection between Central America and South America only about 3 Ma.

The lack of any paleobotanical evidence for significant highlands is in agreement with plate tectonic models suggesting that elevation of the early volcanic islands and peninsulas gradually increased during the latter part of the Cenozoic, and that the highest elevations (3,475 m in the western mountains of Panama; 3,820 m, Cerro Chirripo, Costa Rica) are of recent origin. Altitudes up to about 1,200–1,500 m would accommodate all elements in the four lower Miocene floras known from southern Central America. No pollen was being blown, washed, or transported into the depositional basin to suggest dry vegetation or high altitudes in the Gatuncillo, Uscari, Culebra, Cucaracha, or La Boca formations of Costa Rica and Panama. Muller (1959) demonstrated that pollen from a variety of inland and upland communities is transported by rivers and deposited in coastal basins. Palynological data from Puerto Rico and southern Mexico further show that many of these habitats, represented by both wind- and insect-pollinated elements, are included in the microfossil record if such habitats exist in the region.

All taxa identified from the La Boca Formation except *Crudia* occur in the modern vegetation of Panama. Consequently the paleoenvironment must have been similar to the tropical conditions presently prevailing in coastal, lowland, and moderate-altitude habitats in southern Central America. This is consistent with paleotemperature curves (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975) that show the Uscari, Culebra, Cucaracha, and La Boca floras were deposited during a relatively warm interval just before the significant temperature drop in middle and late Miocene times.

LITERATURE CITED

BAILEY, L. H. 1943. Palmaceae. *In:* R. E. Woodson & R. W. Schery (editors), Flora of Panama. Ann. Missouri Bot. Gard. 30: 327–396.

COWAN, R. S. & R. M. POLHILL. 1981. Detarieae. Pp. 117–134 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford, California.

D'ARCY, W. G. 1987. Flora of Panama Checklist and Index. Monogr. Syst. Bot. Missouri Bot. Gard., Volumes 17, 18.

FERGUSON, I. K. 1986. Observations on the variation in pollen morphology of Palmae and its significance. Canad. J. Bot. 64: 3079–3090.

GASTONY, G. J. & R. TRYON. 1976. Spore morphology in the Cyatheaceae II. The genera *Lophosoria*, *Metaxya*, *Sphaeropteris*, *Alsophila*, and *Nephelea*. Amer. J. Bot. 63: 738–758.

GERMERAAD, J. H., C. A. HOPPING & J. MULLER. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palynol. 6: 189–348.

GONZÁLEZ GUZMÁN, A. E. 1967. A palynological study

on the upper Los Cuervos and Mirador formations (lower and middle Eocene; Tibú area, Colombia). E. J. Brill, Leiden.

GRAHAM, A. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787–842.

———. 1977. New records of *Pelliceria* (Theaceae/Pelliceriaceae) in the Tertiary of the Caribbean. Biotropica 9: 48–52.

———. 1985. Studies in neotropical paleobotany. IV. The Eocene communities of Panama. Ann. Missouri Bot. Gard. 72: 504–534.

———. 1987a. Miocene communities and paleoenvironments of southern Costa Rica. Amer. J. Bot. 74: 1501–1518.

———. 1987b. Tropical American floras and paleoenvironments: Mexico, Costa Rica and Panama. Amer. J. Bot. 74: 1519–1531.

———. 1988a. Studies in neotropical paleobotany. V. The lower Miocene communities of Panama—the Culebra Formation. Ann. Missouri Bot. Gard. 75: 1440–1466.

———. 1988b. Studies in neotropical paleobotany. VI. The lower Miocene communities of Panama—the Cucaracha Formation. Ann. Missouri Bot. Gard. 75: 1467–1479.

——— & G. F. BARKER. 1981. Palynology and tribal classification in the Caesalpinioideae. Pp. 801–834 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

——— & D. M. JARZEN. 1969. Studies in neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

———, R. H. STEWART & J. L. STEWART. 1985. Studies in neotropical paleobotany. III. The Tertiary communities of Panama—geology of the pollen bearing sediments. Ann. Missouri Bot. Gard. 72: 485–503.

HARTSHORN, G. S. 1983. Plants. Pp. 118–157 *in* D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago.

HOLDRIDGE, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105: 367–368.

———, W. C. GRENKE, W. H. HATHEWAY, T. LIANG & J. A. TOSI. 1971. Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, New York.

LANGENHEIM, J. H., B. L. HACKNER & A. H. BARTLETT. 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. Bot. Mus. Leafl. 21: 289–324.

LEOPOLD, E. B. 1969. Miocene pollen and spore flora of Eniwetok Atoll, Marshall Islands. Profess. Pap. U.S. Geol. Surv. 260-II: 1133–1185.

MULLER, J. 1959. Palynology of Recent Orinoco delta and shelf sediments: reports of the Orinoco shelf expedition, 5. Micropaleontology 5: 1–32.

———. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. (Lancaster) 47: 1–142.

———. 1984. Significance of fossil pollen for angiosperm history. Ann. Missouri Bot. Gard. 71: 419–443.

——— & C. CARATINI. 1977. Pollen of *Rhizophora* (Rhizophoraceae) as a guide fossil. Pollen & Spores 19: 361–389.

NILSSON, S. & A. ROBYNS. 1986. Bombacaceae Kunth. Pp. 1–59 *in* S. Nilsson (editor), World Pollen and Spore Flora 14. Almqvist & Wiksell, Stockholm.

SAVIN, S. M. 1977. The history of the Earth's surface temperature during the past 100 million years. Annual Rev. Earth Planet. Sci. 5: 319–355.

——— & R. G. DOUGLAS. 1985. Sea level, climate, and the Central American land bridge. Pp. 303–324 *in* F. G. Stehli & S. D. Webb (editors), The Great American Biotic Interchange. Plenum, New York.

———, ——— & F. G. STEHLI. 1975. Tertiary marine paleotemperatures. Bull. Geol. Soc. Amer. 86: 1499–1510.

STEWART, R. H. & J. L. STEWART (with the collaboration of W. P. Woodring). 1980. Geologic Map of the Panama Canal and Vicinity, Republic of Panama. Scale 1:100,000. U.S. Geol. Surv. Misc. Invest. Map I-1232. [Map also included in Woodring, 1982, Profess. Pap. U.S. Geol. Surv. 306-F.]

TAYLOR, P. 1976. Lentibulariaceae. *In:* R. E. Woodson & R. W. Schery (editors), Flora of Panama. Ann. Missouri Bot. Gard. 63: 565–580.

THANIKAIMONI, G. 1970. Les palmiers: palynologie et systématique. Inst. Franç. Pondichéry, Trav. Sect. Sci. Tech. XI: 1–286.

TRYON, R. M. & A. F. TRYON. 1982. Ferns and Allied Plants, with Special Reference to Tropical America. Springer-Verlag, New York.

TSUKADA, M. 1964. Pollen morphology and identification III. Modern and fossil tropical pollen with emphasis on Bombacaceae. Pollen & Spores 6: 393–462.

VAN DEN BOLD, W. A. 1972. Ostracoda of the La Boca Formation, Panama Canal Zone. Micropaleontology 18: 410–442.

———. 1973. La posición estratigráfica de la formación La Boca, Panama, Zona del Canal. Publ. Geol. ICAITI 4: 167–170.

WEBSTER, G. L. & D. BURCH. 1967. Euphorbiaceae. *In:* R. E. Woodson & R. W. Schery (editors), Flora of Panama. Ann. Missouri Bot. Gard. 54: 211–350.

WOLFE, J. A. 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. 62: 264–279.

WOODRING, W. P. 1957–1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Profess. Pap. U.S. Geol. Surv. 306A–F.

WOODSON, R. E. & R. W. SCHERY. 1943–1980. Flora of Panama. Ann. Missouri Bot. Gard. 30 (1943) et seq.